

Emergence Success of Flatback Sea Turtles (*Natator depressus*) at Fog Bay, Northern Territory, Australia

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ABSTRACT. – The study determined biotic, environmental, and other influences affecting emergence success, hatchling emergence output, and hatchling sex ratio of flatback sea turtles (*Natator depressus*, Garman) at Fog Bay, Northern Territory, Australia. Nests were monitored over two seasons (1997–98) to determine the number of emerged, depredated, or unaccounted nests. Predation by goannas accounted for 52.1 % of all nests. Of the undepredated nests, emergence success was high (94.7%). Hatch success, however, was low early and late in the season. Microorganisms or invertebrates infested few eggs. Nest depth temperatures had a positive association with solar radiation and a negative association with incubation period. High temperatures may be causing high nest mortality between September–November. A female-biased sex ratio was predicted with the period June–August critical for the production of males. The number of hatchlings produced varied spatially and temporally.

KEY WORDS. – Reptilia; Testudines; Cheloniidae; *Natator depressus*; sea turtle; ecology; reproduction; biotic factors; conservation; emergence success; environmental factors; eggs; sex ratio; Australia

Sea turtles are vulnerable to mortality at all stages of their life cycle (Stancyk, 1982). Embryonic development has been accredited as the stage of greatest vulnerability due to unpredictable incubation conditions and the variety of egg predators found on nesting beaches (Limpus and Fleay, 1983; Mrosovsky, 1989). Nesting females expend considerable energy depositing several nests per breeding season in order to produce enough hatchlings to ensure population stability (Miller, 1997).

A useful measure of the success of nesting effort for a population of sea turtles is the output, the proportion of nests that produce emergent hatchlings, and the emergence success, the percentage of eggs in a clutch that produce hatchlings to the sand surface (Hewavisenthi and Parmenter, 2002). Emergence success is determined from the remnants of hatched nests by the following equation (Miller, 1999):

$$\text{Emergence Success (\%)} = 100\% - \frac{\text{shells} - (L + D)}{\text{shells} + UD + UH + UHT + P}$$

Where shells = number of eggshells (hatched eggs), L = number of live hatchlings remaining in the nest, D = the number of dead hatchlings, UHT = number of hatchlings dead in the egg, UH = the number of unhatched eggs with embryo development, UD = the number of unhatched eggs without embryonic development, P = the number of depredated eggs, which is either already known or can be estimated if the number of eggs in the clutch was known prior to excavation, otherwise it is assumed to be zero (Miller, 1999).

Several biotic, environmental, and other factors affect output and emergence success of sea turtles. Of the biotic

factors, large terrestrial predators have the most obvious effects at many rookeries (Stancyk et al., 1980; Limpus et al., 1983a; Sivasundar and Prasad, 1996; Ratnaswamy et al., 1997; Blamires and Guinea, 1998). Other biotic factors include burrowing or subterranean predators, e.g., crabs and invertebrates such as flies (Stancyk, 1982; Johnson et al., 1996; Broderick and Hancock, 1997), plant roots invading eggs (Whitmore and Dutton, 1985; Wyneken et al., 1988; Vanderleley, 1996) and microbial and fungal infections (Whitmore and Dutton, 1985). Environmental influences on hatch and emergence success include lethal temperatures, tidal flooding, salinity and beach erosion (Limpus, 1978; Limpus et al., 1983b; Miller, 1997).

Nest temperature is influenced by sand surface temperatures, nests depth, sand color, grain size, and clutch size (Dutton et al., 1985; Mrosovsky, 1994; Godfrey et al., 1997). Nest temperature may become lethal if above or below 24–33°C (Limpus et al., 1983b; Ackerman, 1997; Miller, 1997) and influences the sex ratio of hatchlings by temperature-dependant sex determination (TSD) with males produced at lower nest temperatures and females produced at higher temperatures. The pivotal temperature, where male to female sex ratio of hatchlings is 1:1, lies between 28.5 and 30°C for most sea turtles (Mrosovsky, 1994; Limpus, 1995). Incubation period usually changes in inverse proportion to nest temperature (Dutton et al., 1985; Mrosovsky et al., 1999) thus it may be possible to statistically predict the sex ratio of hatchlings from the incubation period if the pivotal temperature is known or can be measured in the laboratory (Mrosovsky et al., 1999; Godley et al., 2001). An increased incubation period may increase the exposure to factors causing nest mortality (Whitmore and Dutton, 1985).

Sea turtle eggs laid below the high water mark are likely to suffer mortality from inundation (Bustard et al., 1975; Kraemer and Bell, 1980; Whitmore and Dutton, 1985; Sivasundar and Prasad, 1996). Erosion from an unstable beach, strong winds, rain, global warming, and other nesting turtles cause dunes to collapse and may cause egg mortality by exposing them to tides, air, or high temperatures (Kraemer and Bell, 1980; Hays and Speakman, 1991; Sivasundar and Prasad, 1996; Davenport, 1997).

In addition to biotic and environmental factors, emergence success is influenced by other factors, such as the number of eggs deposited that do not develop (Miller, 1999). Eggs fail to develop for two primary, often not easily distinguished, reasons: 1) early embryonic mortality or 2) infertile eggs. A further complication occurs when eggs are actually infertile but become infested by microorganisms in the nest, consequently being interpreted as eggs suffering early embryonic mortality (Whitmore and Dutton, 1985; Miller, 1999). Hatchling mortality on the beach after emergence may also be high due to predation (often by bird or crabs) or other causes and is of concern for management, as increasing hatch or emergence success is of no value if hatchlings are not reaching the sea (Stancyk, 1982; Limpus et al., 1983b; Whitmore and Dutton, 1985).

If predation on a nesting beach is at a level which could potentially depreciate the population, management strategies such as egg relocation (Stancyk et al., 1980; Ratnaswamy et al., 1997), eradication of predators (Limpus and Fleay, 1983; Ratnaswamy and Warren, 1998), or screening nests (Wyneken et al., 1988; Ratnaswamy et al., 1997) are considered necessary. Before their implementation, however, careful consideration should be given to the various biotic, environmental, and other influences on hatchling emergence, as reducing predation will not benefit the population if counteracted by other forms of mortality.

At Fog Bay, Northern Territory, Australia (12°43'S; 130°20'E to 12°40'S; 130°21'E) flatback sea turtles (*Natator depressus*) nest on the mainland and offshore islands during the dry season, March to October (Guinea et al., 1991; Guinea, 1994a,b), when rain, storms, and cyclones are unlikely. Goannas (*Varanus panoptes*) destroy approximately 60% of nests each season (Guinea, 1994a; Blamires, 1999), but the influence of other biotic, environmental, and other factors remains unquantified. Black-necked storks (*Ephippiorhynchus asiaticus*) and ghost crabs (*Ocypode* spp.) may prey on *N. depressus* hatchlings at Fog Bay (Blamires et al., 1999; Whiting and Guinea, 1999). Both of these predators are assumed to have negligible impacts on the number of hatchlings reaching the sea at the mainland rookery as few black-necked storks have ever been observed on the mainland beaches and, even though the impact of ghost crabs has not been delineated, observations of them preying on flatback eggs and/or hatchlings are sparse. In addition, fewer of the larger more aggressive *Ocypode ceratophthalmus*, rather than the smaller less aggressive *O. cordimana*, are active during the dry season (Guinea 1994a; Blamires 1999).

In this study we investigated the factors impacting on output, emergence success, and hatchling sex ratio of flatback sea turtles at Fog Bay. Wire mesh screens were tested as a predator deterrent. The study aimed to: 1) quantify the relative influences of biotic, environmental, and other factors on *N. depressus* hatching and emergence success, 2) estimate the likely sex ratio of emerged hatchlings throughout the nesting season, and 3) direct future management strategies to areas and times of year where benefits are optimized.

METHODS

The study area was 5 km of mainland beach at Fog Bay, Northern Territory, Australia which was divided into four beaches (1 to 4), 1.0–1.4 km in length (Blamires and Guinea, 1998) and monitored over 2–7 days per two-week period throughout the 1997 and 1998 nesting seasons. Turtle crawls were identified by tracks running from the high water mark to the dunes. Crawls with nests associated were identified and marked by a line perpendicular through the track (Schroeder and Murphy, 1999). The location (beach 1, 2, 3, or 4) and position on the dune (dune base, slope, or crest) of each nest was ascertained according to the criteria of Blamires and Guinea (1998). In order to obtain an index for the incubation period, each nest was classified as having occurred the previous night (i.e., less than one day old), one day to a week old, one to two weeks old, or greater than two weeks old. Those from the previous night had fresh tracks beginning at the current high tide line. Tracks were assumed one week old when not covered by the most recent spring high tide. One to two week old tracks were assumed if they started above the current high tide level at the time of observation but not covered by the last spring high tide and not fresh. Tracks two weeks old were covered by the last spring tides (Schroeder and Murphy, 1999). Most observations were made on tides falling from spring to neap. On the few occasions when observations were made on tides rising from neap to spring, distinctions between nests one to two weeks and two weeks old were difficult, as they were all covered by the last spring high tides, therefore all nests over one week were assumed to be one to two weeks old as nests over two weeks old were rare since they presumably were noticed in previous surveys.

Output. — Nests were monitored each trip to determine their fate, which was classified as: a) hatchlings emerged, b) destroyed by predators, or c) unaccounted for (if no signs of either predation or emergence were observed). Since it was not possible to find the exact location of the unaccounted clutches, the cause of failure in these clutches was not determined. Predation was assumed when nests were found with goanna and/or other predator tracks leading to the nest, and the nest was opened and there were eggshells in close proximity to the nest. Nests that had emerged hatchlings but were subsequently raided by predators were recorded as having hatchlings emerge. Output was calculated as the proportion of total nests that had hatched. To compare and

identify any spatial or temporal differences in hatch success, nests were grouped into their respective beaches and into the nesting intervals: March–May (early nesting season), June–August (peak nesting season) and September–November (late nesting season).

Emergence Success. — Nests from which hatchlings emerged were excavated upon encounter, and their clutches were counted and nest depths measured using a fiberglass tape measure. Eggs found opened were classified as hatched or hatched but dead in the egg (if containing a dead hatchling). Unopened eggs were opened to observe if embryonic development had occurred, thus unopened eggs were either undeveloped or developed but dead in the egg. Distinctions were not made between infertile eggs and eggs suffering early mortality and were both classified as undeveloped. Any hatchlings found in the nest were classified as live in the nest or dead in the nest. Emergence rate was calculated as described by Miller (1999), assuming no eggs in hatched nests were depredated prior to emergence.

Thirteen turtles, encountered nesting over the two seasons (8 in 1997 and 5 in 1998), had their clutches counted, taking caution not to alter the orientation of the eggs and taking no more than three hours from the time of laying to prevent any potential mortality (Limpus et al., 1979). A length of flagging tape (approximately 30 cm) was left in the bottom of the nest, recording the clutch size and date with a permanent marker. After counting, the nests were refilled and covered with wire mesh screens that were removed prior to hatching. The nests were excavated upon hatching and the eggs classified as described above. Emergence rates of protected nests were compared with unprotected nests using a Mann-Whitney U-test.

Biotic and Environmental Influences. — Nest predation was determined as described above and the predator was determined by examining the surrounding tracks. Any undeveloped eggs found in emergent nests were examined for signs of internal or external infestation by bacteria, fungus, insects, or plant root invasion.

Temperatures at the sand surface and at 30, 40, and 50 cm depth (approximately representing the top, middle, and bottom of a flatback nest; Vanderleley, 1996) were recorded every 30 min between October 1995 and October 1998 by a data logger (model 6003A, Unidata Australia, Perth) secured permanently to a metal stake on a dune on beach 2. Solar radiation and air temperature were recorded by radiation probe (model 6501 D/TGH, Unidata Australia, Perth) attached to the data logger. Two data loggers were used alternatively allowing the data to be downloaded in the laboratory. The data were later examined and plotted and data sets causing peaks and troughs outside the standard range were eliminated, as they were considered erroneous.

Data for January (non-nesting season), April (early nesting season), July (peak nesting season), and October (late nesting season) were compared. A critical maximum of 34°C and a pivotal temperature of 29.5°C (Limpus, 1995; Hewavisenthi and Parmenter, 2000) were assumed and indicated on plots of nest depth sand temperatures to identify

if eggs were potentially exposed to lethal temperatures and to predict the likely hatchling sex ratio. Regression analyses were done between incubation time and mean sand temperature at 50 cm during incubation and mean solar radiation and mean sand temperatures at 50 cm (using means estimated for 0500, 0900, 1300, 1700, and 2100 hrs). Multiple regression was used to determine the relationship between nest temperature, clutch size, and incubation period on emergence success. Differences in emergence success between March–May and June–August were compared by an unpaired t-test. Comparisons with September–November were not possible due to insufficient observations.

Since tides regularly reached the dune base along most of beach 3, the influence of tides on hatchling emergence was determined by comparing the number of hatched nests and emergence rates on beach 3 with beaches 2 and 4 by unpaired t-tests. Depredated nests were excluded from analyses and, since the beaches were in close proximity to each other, all environmental variables were assumed constant between beaches. The influence of collapsing dunes was determined by measuring dune slopes, using a clinometer (O/Y, Suunto, Helsinki) in 1997 and 1998 along 500 m of heavily utilized stretches of beaches 2, 3, and 4. Each stretch of beach was divided into 100 m sectors and three measurements were made in each sector to obtain an average per sector. Correlation coefficients were calculated to determine the relationship between changes in mean dune slope and changes in the number of successful nests per sector.

Sex Ratio of Hatchlings. — The maximum and minimum proportion of females produced for each period, year, and beach was determined by applying the temperature data (sand depth = 50 cm) to a hatchling sex ratio–temperature curve (Ackerman, 1997). A curve specific for flatbacks was not available, but since most sea turtles have approximately similar hatchling sex ratios according to nest temperature change (Mrosovsky, 1994; Ackerman, 1997), this curve gives a reasonable estimate of sex ratio extremes using the available temperature data. The number of female hatchlings produced was determined from the emergence success estimates for each period, year, and beach.

RESULTS

The 1997 season had 327 successful nestings by *N. depressus* and 1998 had 164. There was a similar output on the dune base in 1997 (21.1%) and 1998 (19.3%), while output on the dune slope was higher in 1998 (78.9%) than in 1997 (27.3%) (Table 1). There were more nests unaccounted for on the dune base in 1998 (36.6%) than in 1997 (20.3%) but fewer on the dune slope (5.3% in 1998; 18.2% in 1997) (Table 1). Beach 2 produced the most emerged nests in both seasons and the majority of nests were deposited between June and August in both seasons on all beaches (Table 2). The number of nests unaccounted for was greatest between September and November in 1997 (Table 2). In 1998 more nests were unaccounted for between June and August, but there were only 15 nests deposited between September and

Table 1. Summary of *Natator depressus* nests deposited, depredated, emerged, and unaccounted for at each location. DB = dune base; DS = dune slope or crest. Table shows data from each season (1997 and 1998). Percentages are in parentheses. Unaccounted nests were not excavated and may have represented clutches that either did not develop, succumbed to subterranean predation or infestation, or hatched but failed to emerge.

Year	Loc.	Nests Deposited	Nests Depredated	Emerged Nests	Unaccounted Nests
1997	DB	261	153(58.6)	55(21.1)	53(20.3)
1997	DS	66	36(54.5)	18(27.3)	12(18.2)
1998	DB	145	64(44.1)	28(19.3)	53(36.6)
1998	DS	19	3(15.8)	15(78.9)	1(5.3)
Total		491	256 (52.1)	116 (23.6)	119 (24.2)

November in 1998 and 13 of them were unaccounted for (Table 2).

Emergence Success. — Eighty-five emerged nests (47 in 1997 and 38 in 1998) were excavated and their clutches counted. Mean emergence success in March–May (95.4%; SD = 5.06; $n = 10$) was not significantly different ($t = 0.34$, $df = 83$, $p = 0.73$) from mean emergence success in June–August (93.7%; SD = 11.68; $n = 73$) (Table 3). The majority of nests excavated were on the dune base. No nests on the dune slope were excavated due to dune instability (one nest on the dune crest was excavated and had 100% emergence success). The Mann-Whitney U-test found no significant difference in emergence success between nests protected with wire screens and unprotected nests ($U = 438.5$, $Z = 0.365$, $p = 0.719$).

Biotic and Environmental Influences. — Predation was lower in 1998 (41%) than in 1997 (58%); accounting for 52.1% for both years combined (Table 1). Nests on beach 2 suffered the least predation in both seasons. Every depredated nest observed was surrounded by goanna tracks so goannas were assumed the predominant predator of nests over the study period, although predation by other predators (e.g., ghost crabs, water rats) should not be ruled out. The number of eggs infested by bacteria, fungus, or insects per

Table 2. Summary of *Natator depressus* nesting at the Fog Bay rookery for each three-month period in the 1997 and 1998 nesting seasons. Total crawls, nests deposited, depredated, emerged, and unaccounted are shown (B1–B4 = beaches 1–4).

		1997				1998			
		B1	B2	B3	B4	B1	B2	B3	B4
Crawls:	Mar-May	0	21	25	22	1	17	6	21
	Jun-Aug	3	46	25	104	0	45	36	66
	Sep-Nov	2	22	29	54	0	13	4	8
Deposited:	Mar-May	0	19	25	22	0	13	3	15
	Jun-Aug	3	42	24	100	0	36	25	57
	Sep-Nov	1	16	28	51	0	9	2	4
Depredated:	Mar-May	0	13	19	14	0	4	2	9
	Jun-Aug	0	7	20	68	0	9	13	28
	Sep-Nov	0	7	13	28	0	1	0	1
Emerged:	Mar-May	0	4	3	0	0	8	0	5
	Jun-Aug	0	35	2	24	0	20	0	10
	Sep-Nov	0	3	0	2	0	0	0	0
Unaccounted:	Mar-May	0	2	3	8	0	1	1	1
	Jun-Aug	3	0	2	8	0	7	12	19
	Sep-Nov	1	6	15	21	0	8	2	3

Table 3. Mean (\pm S.D.) clutch size and emergence success (overall and for each year, beach and period; when measured) for undepredated *Natator depressus* nests at Fog Bay in 1997 and 1998. Mean nest depth for all 85 nests = 56.9 ± 9.8 cm.

	<i>n</i>	Clutch Size	No. Emerged	Emergence Success
Overall	85	51.6 (8.64)	48.9 (10.16)	94.7
1997:	47	52.7 (7.24)	50.3 (6.75)	95.5
1998:	38	50.1 (10.23)	46.9 (9.28)	93.6
Beach 2:	47	51.7 (9.68)	47.9 (10.74)	92.6
Beach 3:	5	51.2 (14.93)	45.9 (16.4)	89.7
Beach 4:	33	51.6 (3.52)	50.1 (7.04)	97.1
Mar-May:	10	52.7	50.3 (5.06)	95.4
Jun-Aug:	73	50.2	47.0 (11.68)	93.7
Sep-Nov:	2	52.0	50.5 (4.0)	97.0

nest was between 0 (64 nests; 75.3%) and 26 (mean = 1.12; SD = 3.37). Eighty-one (95.3%) nests had less than five eggs infested. No evidence of plant root invasion of eggs was found.

The average air, sand surface, and nest depth (50 cm) temperatures for four times of year (January, April, July, and October) are shown in Fig. 1. The sand surface had the greatest mean temperature fluctuations and the greatest extremes at all times of year. Mean air temperature was the most stable in October. Sand temperatures fluctuated the least at 50 cm, although there was variation between the four times of year, with the lowest temperatures recorded in July and the greatest in April.

Temperatures recorded at 30 cm (top of nest), 40 cm (middle of nest), and 50 cm (bottom of nest) for both nesting seasons (Table 4) show sand temperatures in 1997 were slightly warmer but had similar extremes. The two seasons data were pooled in Fig. 2 showing mean temperatures in January (non-nesting season), April (early nesting season), July (mid-nesting season), and October (late nesting season). Maximum temperatures at 30 cm were the highest in October but extremes of over 34°C appeared at all times of year. In January, April, and October only values at 30 and 40 cm were lower than the pivotal temperature but in July, mean values at all depths were around the pivotal temperature.

The mean incubation period was 53.2 days (SD = 10.91). A negative relationship was found between sand temperature at 50 cm (TS_{50}) and incubation period ($r = -$

Table 4. Means, minimums, maximums, and standard deviations for sand temperatures (°C) at Fog Bay for the 1997 and 1998 nesting season. Depths were 30 cm (TS_{30}), 40 cm (TS_{40}), and 50 cm (TS_{50}), representing the top (30 cm), middle (40 cm) and bottom (50 cm) of an average *Natator depressus* nest. All measurements were made at a standard non-nest location on the dune crest of beach 2.

	<i>n</i>	Mean	Min	Max	S.D.
1997					
TS_{30}	13493	31.81	28.2	34.8	1.755
TS_{40}	13493	31.38	29.7	33.4	0.945
TS_{50}	9943	31.71	30.1	33.5	1.009
1998					
TS_{30}	9772	30.79	28.2	34.8	1.591
TS_{40}	8231	30.72	29.4	33.2	0.849
TS_{50}	4027	31.20	29.8	33.5	0.888

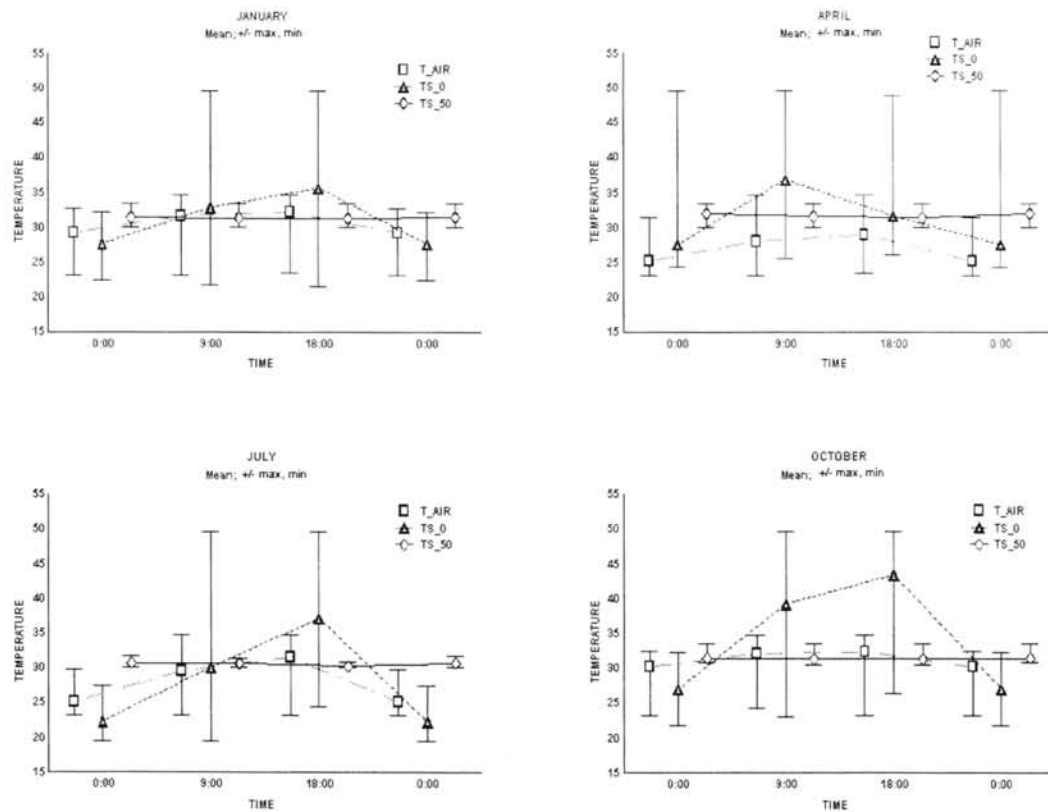


Figure 1. Mean air and sand temperature at the surface and 50 cm depth throughout the day at four times of year. T_AIR = air temperature, TS_0 = sand surface temperature, and TS_50 = sand temperature at 50 cm, and January, April, July, and October represent the non-nesting, early nesting, peak nesting, and late nesting periods, respectively. Error bars (whiskers) = \pm max, min values.

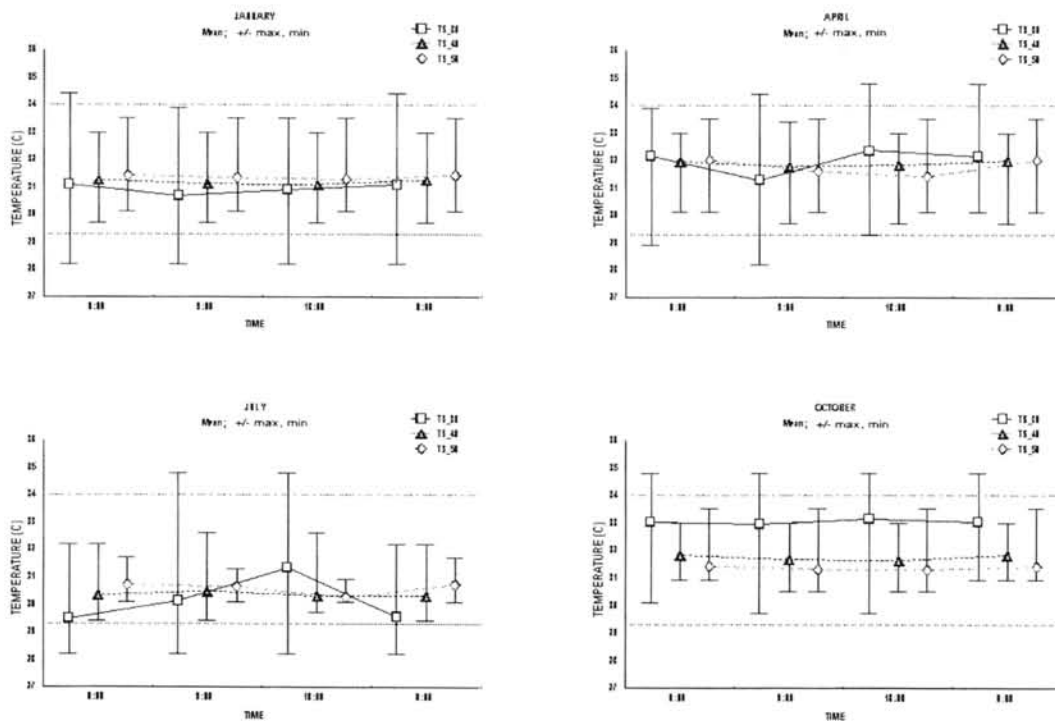


Figure 2. Mean sand temperatures at 30, 40, and 50 cm depth throughout the day, at four times of year. TS_30 = sand temperature at 30 cm, TS_40 = sand temperature at 40 cm, and TS_50 = sand temperature at 50 cm, and January, April, July, and October represent the non-nesting, early nesting, peak nesting, and late nesting periods, respectively. Error bars (whiskers) = \pm max, min values.

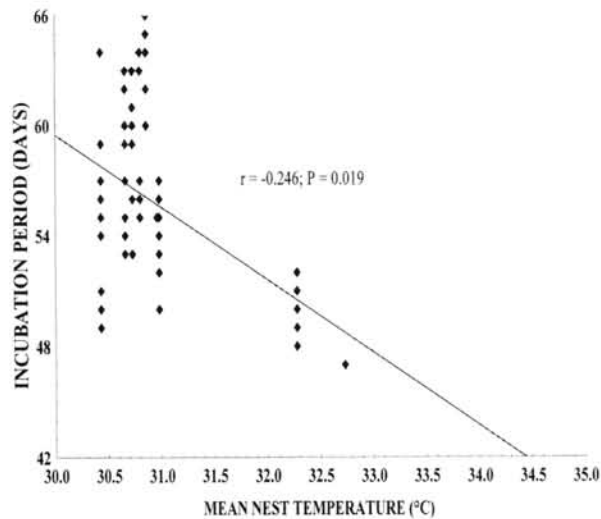


Figure 3. Results of regression analysis between incubation period and mean sand temperature at 50 cm (T_{s50}). Regression equation: Incubation Period = $264.5 - 6.99 \times T_{s50}$.

0.246; $p = 0.019$; Fig. 3). Multiple regression found no significant influence of mean nest temperature ($r = 0.018$; $p = 0.38$), clutch size ($r = 0.005$; $p = 0.623$), and incubation period ($r = 0.001$; $p = 0.772$) of emerged nests on emergence rates ($R^2 = 0.246$; $p = 0.298$). Solar radiation ($\text{cal. cm}^{-2}\text{min}^{-1}$) had a significantly positive correlation with T_{s50} ($r = 0.604$; $p < 0.001$; $T_{s50} = 30.87 + 0.002 \times \text{solar radiation}$).

No significant differences were found between the number of emerged nests on beaches 2 and 3 ($t = -1.97$; $df = 10$; $p = 0.077$) and beaches 3 and 4 ($t = -1.57$; $df = 10$; $p = 0.146$) when nests lost to predation were excluded from analyses. Beach 3 had a significantly lower emergence success than beach 4 ($t = 2.59$; $df = 37$; $p = 0.01$). Beaches

2 and 3, however, did not have a significantly different emergence success ($t = 0.57$; $df = 50$; $p = 0.57$). Changes in the number of nests laid in 1997 and 1998 was not significantly correlated with changes in dune slopes ($r = 0.266$; $p = 0.338$).

Sex Ratio of Hatchlings. — For each period, beach, and year, the total number of predicted hatchlings (Table 5) and the number of predicted females that may have been produced (Table 6) was determined. In 1997 a range of 1361 to 3675 (37–100%) female hatchlings may have emerged from hatched nests and in 1998 a range of 605–2015 (30–100%) may have emerged (Table 6).

DISCUSSION

On beach 3 only five clutches emerged of 107 deposited throughout the 1997 and 1998 seasons and, of the 102 failing to hatch, predation accounted for 67 with 35 failing to emerge for unknown reasons. As the beaches were surveyed in the morning (0630–0900 hrs) when hatchling and/or predator tracks are most visible (Blamires, 2000) it is unlikely that the nests hatched or were depredated but not recorded. It may be possible that flooding was responsible as along the southern-most 500 m of beach 3 the spring high tide often reaches the dune base and flatbacks have difficulty accessing the dune slope and crest due to the steepness of the dune and a layer of rock at the base. Given that one-in-eight nests on beach 3 produced hatchlings, only 9 or 10 of the 67 depredated nests might have emerged. Beach 2, on the other hand, had 70 nests emerge of 94 that were not depredated and beach 4 had a two-in-five emergence output. Beach 3 therefore was considered a comparatively unproductive beach at Fog Bay.

Mean clutch sizes and nest depths were similar to those documented for other *N. depressus* populations (Limpus, 1971; Limpus et al., 1981; Limpus et al., 1983c; Vanderleley, 1996; Hewavithenth and Parmenter, 2002). Emergence success, however, was higher than those reported for other *N. depressus* populations (Limpus et al., 1981; Limpus et al., 1983c; Vanderleley, 1996). At this rookery the number of nests failing to emerge due to predation or other causes is of greater concern than the number of hatchlings emerging from hatched nests. High emergence success may be indicative of favorable incubation conditions at Fog Bay between June and August on beaches 2 and 4; this supposition, however, requires validation. It appears, nonetheless, that avoiding nest predation between June and August on beaches 2 and 4 could have a significantly positive effect on the number of hatchlings reaching the sea.

Predation by goannas was the major form of nest mortality throughout the 1997 and 1998 nesting seasons, accounting for 52.1% of all *N. depressus* nests, which is lower than previous predation estimates for Fog Bay (60–67%; Guinea, 1994a; Blamires and Guinea, 1998). Research quantifying the population status of flatbacks at Fog Bay (incorporating the nearby islands) is urgently required to determine if the level of predation measured here is of a

Table 5. Predicted total number of hatchlings emerging on each beach in each period. (B1–4 = beaches 1–4).

		B1	B2	B3	B4
1997	Mar-May	0	201	151	0
	Jun-Aug	0	1762	101	1208
	Sep-Nov	0	151	0	101
1998	Mar-May	0	375	0	234
	Jun-Aug	0	937	0	469
	Sep-Nov	0	0	0	0

Table 6. The maximum (Max T_n) and minimum (Min T_n) sand temperatures at 50 cm depth and the percentage of female hatchlings predicted (% female) in each period.

		Max T_n	Min T_n	% female
1997	Mar-May	29.7	34.8	65–100
	Jun-Aug	28.2	32.6	30–100
	Sep-Nov	30.5	34.8	85–100
1998	Mar-May	28.3	34.9	30–100
	Jun-Aug	28.2	32.8	30–100
	Sep-Nov	29.8	33.0	72–100

potentially depreciative threat. If the levels are considered to be of concern, the implementation of management may be warranted, taking into account the relative influences of biotic, environmental, or other forms of nest mortality.

There were few eggs found infested by bacteria, fungus, or insects, none were invaded by plant roots, and few hatchlings were found dead in the nest or egg, compared to some other sea turtle rookeries (Wyneken et al., 1988; Vanderleley, 1996; Broderick and Hancock, 1997). In other *N. depressus* populations at least 1% of eggs deposited fail to develop obvious embryos (Limpus, 1971; Limpus et al., 1981, 1983c), so relatively few of the undeveloped eggs would have been likely to have had embryos that died early in development.

Few nests hatched between September and November when maximum temperatures above 34°C at 30 cm sand depth were common. Even though temperature did not effect emergence success in nests from which hatchlings emerged, at temperatures above 34°C sea turtle eggs are not expected to survive incubation (Limpus et al., 1983b; Miller, 1997). A high number of unaccounted nests between September–November may be a result of the upper layer of eggs being placed approximately 30 cm below the sand surface (Vanderleley, 1996) and consequently being exposed to lethal temperatures. Eggs may be hatching in the nest but hatchlings may fail to emerge because of exposure to lethal temperatures as they approach the sand surface or are suffocating due to oxygen depletion as a consequence of high incubation temperatures (Ackerman, 1977).

Tall, steep dunes line the Fog Bay coastline and the sun rising from the east causes significant shadowing of the dune base during most of the morning. Shadowing over the dune base may decrease the rate of nest warming (Mrosovsky et al., 1995) and by placing the majority of nests at the dune base, *N. depressus* nest temperatures may be considerably lower than indicated by the data logger placed on the dune crest of beach 2, causing misinterpretation of actual thermal influences on nest mortality. Despite this, constantly high temperatures recorded in September–November strongly coincide with the times of lowest nest survivorship and remain the most likely explanation for a high proportion of nests being unaccounted for at this time. It is recommended that the influence of lethal temperatures and shading on *N. depressus* nesting success at Fog Bay be investigated further.

A negative correlation between nest temperature and incubation period was found, as demonstrated in other sea turtles (Miller, 1997). Nest temperature was strongly correlated to solar radiation, although there is a time lag between the surface sand warming and sand at nest depth warming at Fog Bay (Guinea, 1994b). Emergence success was not dependent on incubation period and clutch size, thus splitting clutches or nest shading would not improve the emergence success of hatchlings in the emerged nests.

Beach 3 had a significantly lower emergence success than beach 4. As stated previously, inundation appears to contribute to the complete failure of many nests on beach 3. The lower emergence success on beach 3 may also be

attributed to inundation, as nests not entirely destroyed may have had fewer eggs survive to produce emergent hatchlings. Emergence success, however, was not significantly lower on beach 3 than beaches 2 or 4, when excluding nests lost to predation. Predation was thus assumed to be the principal cause of egg mortality on all beaches and of greatest concern for any future management at Fog Bay. The reason for the notably low emergence success on beach 3 is not clear but could warrant the relocation of all nests placed on this beach. Dune collapse through erosion may have long-term consequences on sea turtle nesting (Limpus and Fleay, 1983) and thus should be continuously monitored at Fog Bay, but there was no evidence that it influenced emergence success in this study.

Nest depth sand temperatures never remained low enough to suggest many males were produced in either season. In 1998 there may have been less of a female bias since nest temperatures were cooler in March–May producing more males and no hatchlings emerged between September–November when nests were the warmest, however, higher hatchling output suggests there were more males produced overall in 1997. Based on temperatures recorded at 50 cm sand depth, the period from June to August appeared the most critical for producing males. Female-biased hatchling sex ratios have been found for *N. depressus* at Mon Repos (Limpus, 1995) and Kakadu (Vanderleley, 1996) without there being known detrimental effects to the nesting population. The minimum number of males that can be produced without compromising future breeding populations is unknown but biases of over 90% female have been estimated for apparently stable populations of loggerheads (Marcovaldi et al., 1997) and hawksbills (Godfrey et al., 1999) in Brazil. It is recommended that *N. depressus* nest temperatures be monitored at Fog Bay, incorporating the offshore islands, to predict the likely hatchling sex ratio, ensuring there is production of both sexes. Experiments determining the pivotal temperature for *N. depressus* specific for Fog Bay will enable more accurate estimations of sex ratio derived from incubation periods (Mrosovsky et al., 1999), relieving the requirement of using data loggers.

Conservation Implications

If predation rates were regarded severe enough to warrant the implementation of management strategies at Fog Bay, they would only be effective in increasing hatchling output under certain conditions at certain times. Effective management strategies depend largely on controlling a nest predator (Stancyk et al., 1980). Eradication of native wildlife is usually contradictory to wildlife management, unless removal of an abundant native species is of benefit to a threatened native species and other avenues of conservation are not plausible (Ratnaswamy et al., 1997; Ratnaswamy and Warren, 1998). Relocation risks movement-induced mortality (Limpus et al., 1979) and placing eggs into unpredictable environments (Whitmore and Dutton, 1985), therefore is used only if nest protection *in situ* is not possible, e.g., if laid

below spring high water (Whitmore and Dutton, 1985; Hays and Speakman, 1991; Ratnaswamy et al., 1997). Low output suggests that all nests deposited late in the season and on beach 3 could be considered doomed and relocation strategies implemented.

Covering nests with wire mesh screens appeared to be an effective protection strategy at Fog Bay as it prevented goanna predation and did not affect the emergence success of the nests. However, this technique requires encountering nesting turtles and low nesting densities may make finding turtles difficult at certain times of year and benefits may not outweigh the costs involved. Additionally, there is evidence that at some rookeries this technique is detrimental to emergence success (Murphy and Bjork, 1996) and that using wire can alter the surrounding magnetic field, interrupting the natal imprinting sense of hatchlings (Admany et al., 1997). If 50% of the nests lost to predation between June–August over the two years of this study were protected, about 70 extra nests could have produced emerged hatchlings, producing about 3500 more hatchlings into the sea. Based on a survivorship from nest to maturity of approximately 1 in 400 for *N. depressus* (Parmenter and Limpus, 1995), this could have produced about nine future breeding adults per year. This figure depends largely on the status and density of the population (Parmenter and Limpus, 1995) and may be greater for the Fog Bay population. It is recommended that other sea turtle rookery managers understand the status of the nesting population in question and measure the biotic, environmental, and other influences on output, emergence success, and hatchling sex ratio before implementing strategies.

ACKNOWLEDGMENTS

We thank S. Whiting and M. Nobbs for assisting with data collection and J. Herbert and M. Thompson for use of computing facilities. We also thank the management at the Lodge of Dundee and H and K Earthmoving for permission to access the study site and accommodation, and all volunteers who generously donated their spare time to assist in the field. We thank D. Booth, K. Christian, and G. Thompson for comments on earlier versions of the manuscript and C. Limpus and an anonymous referee for their constructive comments. Research was funded by Australian Geographic, The Queen's Trust for Young Achievers, and The Centre for Tropical Wetlands Management, Northern Territory University.

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Received: 19 December 2000

Revised and Accepted: 15 July 2002