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Influence of Nest Site Selection on Predation of Flatback Sea Turtle (*Natator depressus*) Eggs by Varanid Lizards in Northern Australia

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ABSTRACT. – We examined nest site selection of flatback sea turtles (*Natator depressus*) at two sites: Fog Bay, Northern Territory, and Mundabullangana, Western Australia. Nesting at Fog Bay occurred predominantly at the dune base. The dunes at Fog Bay are tall and steep, while the dune slopes at Mundabullangana are less severe and their crests are more accessible. Apart from afternoon nesting at Mundabullangana, *N. depressus* nesting procedure was similar at both sites: nesting around high tide, with reasonably direct crawls up the beach and the choice of nesting site unaffected by turtle size. At Fog Bay attempts to climb the dune usually resulted in no nesting and gradient of the dunes appeared to confine nesting to the dune base. At Fog Bay many nests were raided by the goanna, *Varanus panoptes*. There was no significant difference in natural egg predation on the dune base or slope at Fog Bay. An experiment, using hen's eggs, showed simulated nests on the dune crest were raided more frequently than at the dune base, on both nesting and non-nesting beaches. Vision and chemoreception have been implicated as cues used by the goannas.

KEY WORDS. – Reptilia; Testudines; Cheloniidae; *Natator depressus*; sea turtle; Lacertilia; Varanidae; *Varanus panoptes*; nest predation; nest site selection; predator deterrence; conservation; Australia

The flatback sea turtle, *Natator depressus*, usually nests at night around high tide (Bustard et al., 1975; Limpus et al., 1981) although daytime emergence may occur at some rookeries (Bustard et al., 1975; Limpus et al., 1981, 1983a, 1989). Nesting around high tide may help *N. depressus* overcome offshore obstacles such as mud banks or exposed reefs. Although deliberate for a sea turtle (Bustard et al., 1975; Miller, 1997), *N. depressus* crawls up the beach relatively slowly, stopping frequently for breath and orientation (Bustard, 1972).

Once on the beach, a turtle must select a site to nest or return to the water and attempt to nest somewhere else on the nesting beach (Chan and Liew, 1989). Turtle size influences nesting energetics in leatherback sea turtles (*Dermochelys coriacea)* (Spotila and Standora, 1985) but not necessarily the decision of where to nest (Eckert, 1987). Encountering the berm-scarp interval or the presence of vegetation on the dune are possible cues used by female flatback sea turtles to initiate nesting (Bustard, 1972). This however, does not explain why they often continue to crawl further after encountering the dune bank or why they often nest in areas devoid of vegetation (Bustard, 1972; Bustard et al., 1975). Sand structure and depth, salinity, beach elevation, and temperature profile have been argued equally for and against as cues that influence the decision of where to nest in sea turtles (Stoneburner and Richardson, 1981; Horocks and Scott, 1991; Hays and Speakman, 1993; Wood and Bjorndal, 2000). Once she has selected her nesting site the turtle digs her egg chamber and, unless disturbed or impeded by obstacles, she will lay (Bustard, 1972; Bustard et al., 1975; Miller, 1997). If nesting is abandoned a turtle may re-attempt to nest later the same night or on subsequent nights, with the probability of nesting occurring at non-preferred sites increasing on each subsequent attempt (Bustard et al., 1975; Miller, 1997; Horrocks and Scott, 1991).

At the mainland beaches of Fog Bay, approximately 150 km southwest of Darwin (12°43'S; 130°20'E), Northern Territory, Australia, *N. depressus* nests between March and October (the dry season) in relatively low density (Guinea, 1994; Blamires and Guinea, 1998, 2003). Nesting is predominantly at the dune base (Blamires and Guinea, 1998, 2003), which is uncharacteristic of *N. depressus* from other locations where they generally nest high on the primary dune, or beyond it if accessible (Limpus, 1971; Bustard et al., 1975). The dunes of Fog Bay vary in height from 1 to 13 m with slopes of at least 25°, becoming as steep as 80° in places, thus dune topology may confine most of the nesting to the dune base (Blamires et al., 2001). Dune base nesting may on the other hand be a behavioral trait specific to the Fog Bay population. To determine if nest site selection in *N. depressus* at Fog Bay is typical of this species we compared it with a population from Mundabullangana, Western Australia, where the dunes were less precipitous. Although such a comparison cannot infer where *N. depressus* would nest if greater access to the dune slope was permitted at Fog Bay, it can be used to dissimilate behaviors depicted when crossing the beach slope compared with behaviors depicted when traversing the dune and nesting between two geographically different sites.

The Mundabullangana rookery is approximately 60 km southwest of Port Hedland, Western Australia (20°31'S; 118°04'E) and experiences dense nesting by *N. depressus* during the wet season (October–February) (Prince, 1994). The primary dunes are at a similar distance from the water as at Fog Bay. On the main nesting beach there is a small primary dune, backed by an often larger and steeper secondary dune up to 20 m distant. This rookery thus appears an ideal location for comparing nest site selection behavior of *N. depressus* with the Fog Bay population as turtles here may nest as far beyond the primary dune as they choose to crawl.

At some rookeries, nesting at certain locations may increase the exposure of nests to predation by varanid lizards (goannas, *Varanus* spp.); a major nest predator on many Australasian rookeries, including Fog Bay (Limpus et al., 1983b; Sivasundar and Prasad, 1996; Vanderleley, 1996; Blamires and Guinea, 1998, 2003). A range of strategies have been proposed to minimize nest loss to predation at several rookeries (Limpus and Fleay, 1983; Blamires and Guinea, 2003). Before implementing predator deterrent strategies at the Fog Bay rookery, the viability of the various strategies needs to be tested. The most appropriate strategy would depend on the cues used by the predator to locate nests, for example, relocation may be viable against predators relying on olfaction (Stancyk et al., 1980), but nest screens or hatcheries may be necessary against predators that visually locate nests (Dutton et al., 1985; Ratnaswamy et al., 1997).

Herein we examined nest site selection behavior of *N. depressus* at Fog Bay and Mundabullangana and the subsequent implications of nesting site on predation by the goanna *Varanus panoptes* at Fog Bay. We did not attempt to identify cues used by turtles to initiate nesting. The study aimed to: 1) determine if the behavior associated with nest site selection of *N. depressus* differs between Fog Bay and Mundabullanga, 2) to quantify the influences acting on nest site selection at Fog Bay, and 3) determine the susceptibility of nests to goanna predation at various locations on the dune at Fog Bay and the implications for management.

METHODS

Observations of nest site selection were made at two sites: the Fog Bay and Mundabullangana rookeries. Observations were made at Fog Bay over two nesting seasons (1997 and 1998), during twice-monthly visits lasting two to seven days, and at Mundabullangana 7–20 December 1998. The beach at Fog Bay faces west (approximately 270°) and the Mundabullangana beach faces northwest (approximately 330°). At Mundabullangana an offshore reef flat is exposed when the tide height is less than approximately 3 m. The maximum spring high tide range is approximately 8 m at Fog Bay and approximately 7 m at Mundabullangana. The tidal regime at both beaches is semi-diurnal. The beaches of both sites were walked at night during high tide and during the day.

The time of emergence of any turtles encountered nesting was noted. Characteristics of the inbound crawl (incrawl) were described by a series of measurements on tracks left on the beach by turtles that emerged the previous night (Schroeder and Murphy, 1999). Only tracks not traversed by other turtle tracks, thus easily followed to the nest or back to sea, were measured. The direction from the point of emergence (or the previous night's high water mark) to the initial body pit was determined by compass and the mean directions were determined by statistics of circular distribution (Zar, 1984). The distance crawled before the initial body pit was measured along the midline of the track by flexible tape measure to the nearest meter. All changes in crawl direction were recorded. Nesting was identified according to Schroeder and Murphy (1999) and recorded. When a turtle crawled up the beach and returned to the sea without digging a body pit (false crawl), the total crawl distance was measured. For tracks with multiple body pits, the distance and direction of each intermediate crawl was measured. Possible disturbances causing failure to nest were noted.

To determine if the size of the nesting turtles influenced where they chose to nest, the curved carapace length (CL) of all turtles encountered nesting at Fog Bay and Mundabullangana were measured to the nearest 0.5 cm with a flexible measuring tape (Limpus et al., 1983a, 1989). For turtles encountered at Mundabullangana, the nest location was classified as at the base of the primary dune, on the crest of the primary dune or on the secondary dune. Mean CL of turtles nesting at the base of the primary dune were compared with those nesting on the crest of the primary dune by an unpaired t-test. The mean CL of turtles nesting at the base of, and on the primary dune were pooled and compared with mean CL of turtles nesting on the secondary dune using an unpaired t-test. All turtles encountered were tagged in both fore-flippers with numbered titanium flipper tags to ensure no turtles were repeatedly measured.

All nests constructed at Fog Bay were classified as being: on the dune base, on the dune slope, or on its crest. Nests were considered lost to predation when found opened with goanna tracks around the nest and > 40 eggshells found in the immediate vicinity of the nest (Blamires and Guinea, 1998, 2003). The beaches were divided according to natural boundaries into four separate beaches, named beach 1, 2, 3, and 4 (as described in Blamires and Guinea [1998, 2003] and Blamires et al. [2001]). Beach 1 experienced very few nests (one or two per year), as did the southern-most 600 m of beach 2. Beaches 3 and 4 were frequently nested upon each season, as was the northern-most 800 m of beach 2. Predation rate was calculated as the percentage of nests lost to predation at each nesting site. The effect of nesting site on predation rate was determined by a Mann-Whitney U-test. Only nests on the dune base and dune slope were compared as too few nests were laid on the dune crest for statistical analysis.

To assess the egg finding ability of goannas at Fog Bay, simulated nests, containing 10 domestic hen's eggs, buried at 30 cm depth, were created at four separate locations along the beach at the dune base and crest. Despite evident differences in odor and texture from flatback sea turtle eggs, varanid lizards are apt at locating eggs of several bird and reptile species (King and Green, 1999) therefore hen's eggs were deemed practical to simulate natural foraging. The experiment was done early in the nesting season (March–April), when it was assumed goannas would be searching for eggs, but low numbers of natural nests would not adversely influence the experiment. Two of the experimental sites were on stretches of beach where *N. depressus* is not known to nest (on beaches 1 and 2) while the other two were in areas that are often nested upon (beaches 3 and 4). Numbered survey flags denoted the location of experimental plots. Treatments were as follows: 1) a hole dug to 30 cm with 10 hen's eggs placed in it and refilled ("eggs" treatment); 2) a hole dug to 30 cm and refilled without eggs ("no eggs" treatment); and 3) no hole or eggs ("flag only" treatment). Three replicates were done for each treatment thus nine plots were made on the dune crest and at the dune base at each of the four site for a total of 72 plots.

A four-way nested ANOVA was done to determine the influence of nest site on predation of these simulated nests. Factors were: 1) beach (1, 2, 3, or 4), 2) beach type (nesting or non-nesting), 3) location (dune base or dune crest), and 4) treatment (eggs, no eggs, or flag only). Predation was scored as 1 = predation or 0 = no predation. Beach was nested within beach type (beaches 1 and 2 within non-nesting and beaches 3 and 4 within nesting). A Tukey's HSD test ($p = 0.05$) was done to determine which sets of means differed and the variables causing them to differ.

RESULTS

At Fog Bay 13 *N. depressus* were encountered successfully nesting, all occurring within 3 hrs of high tide between 2100 and 0600 hrs, although one unsuccessfully attempted to nest at approximately 0800 hrs. At Mundabullangana 241 *N. depressus* were observed nesting with emergence times between 1555 and 0605 hrs. All emergences occurred within 3.5 hrs before or after the high tide, presumably since at this time the reef flat was covered enabling turtles access to the beach, although they often crawled back out to sea over the dry reef flat up to 4.5 hours after high tide. Fifty-four turtles were observed nesting during the afternoon (1555 to 1900

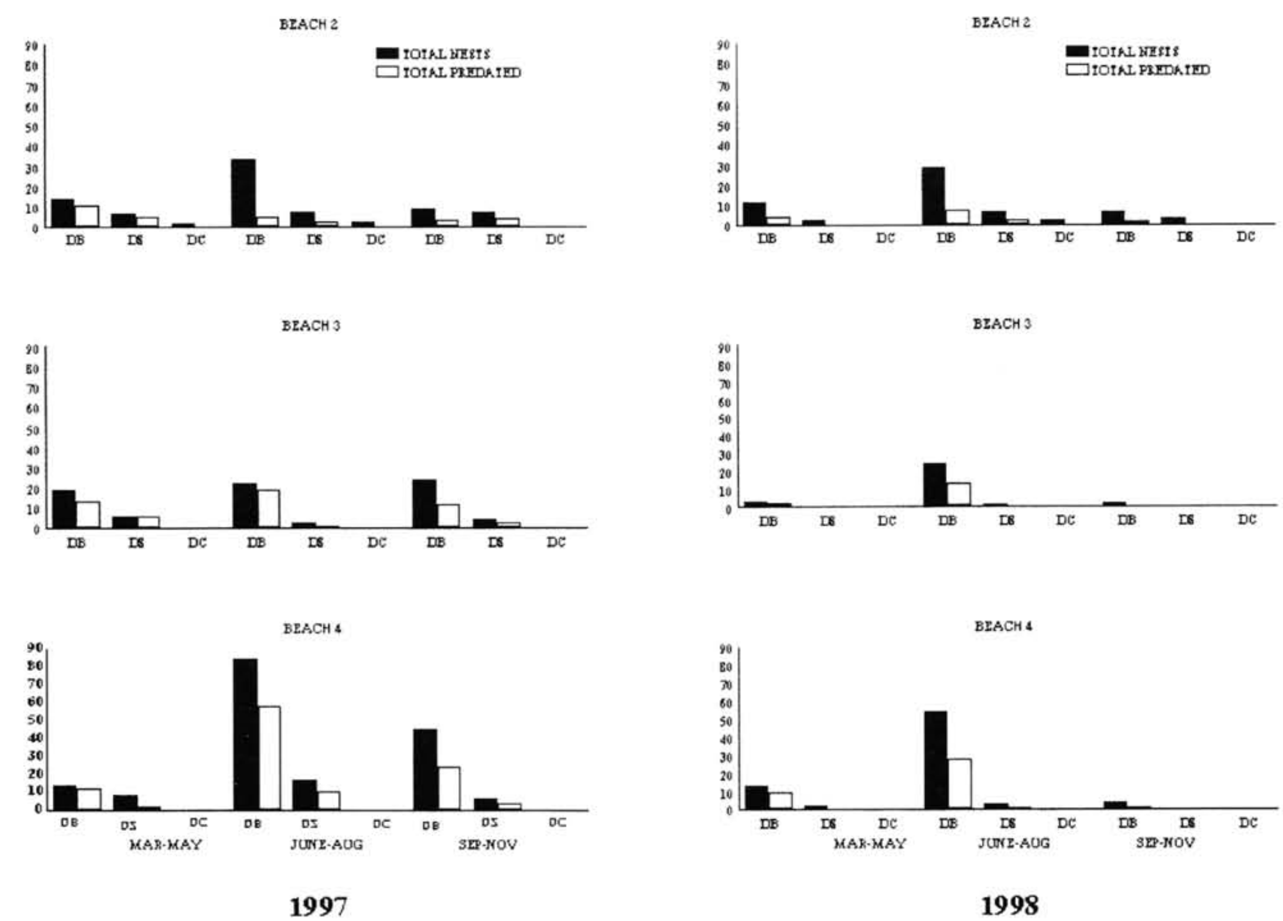

Figure 1. Total clutches laid and number of nests depredated at Fog Bay for the1997 and 1998 nesting seasons, for the periods: Mar–May, June–Aug, and Sep–Nov and at the locations: dune base (DB), dune slope (DS), and dune crest (DC).

Table 1. Numbers of simulated nests (n = 3 for each treatment) raided by goannas in hen's egg predation experiment for "Eggs," "No Eggs," and "Flag Only" treatments according to beach (1, 2, 3, or 4), beach type [nesting (N), non-nesting (NN)] and location (DC = dune crest, DB = dune base).

Beach (type)	Treatment					
	Eggs		No Eggs		Flag Only	
	DC	DB	DC	DB	DC	DB
1(NN)	2	0	1	0	0	0
2(NN)	0	1	1	0	0	0
3(N)	3	1	3	1	0	0
4(N)	0	0	1	1	0	0

hrs) on a falling neap tide and 0 turtles nested during morning high tides.

Twenty-eight tracks at Fog Bay and 12 at Mundabullangana were measured. Eighteen tracks at Fog Bay and 8 at Mundabullangana were associated with successful nests. The mean crawl direction of tracks at Fog Bay was 102°, a 12° deviation from straight up the beach. At Mundabullangana, the mean crawl direction was 153°, a deviation of 3° from straight up the beach. These emergence directions coincide with directions of the surf observed at the respective beaches during the study period. Emergence, thus crawl, direction may be influenced by the surf, although it could not be determined if it physically lifts the turtles or is used as an indicator to direct emergence, additionally it was not ascertained if the direction of emergence reflects the track measurements, which were made from the previous night's high tide line. Mean distance of false crawls was 71.2 m (SD = 31.9; n = 5; range = 19–97 m) at Fog Bay and 38.4 m (SD = 5.0; n = 3; range = 36–44 m) at Mundabullangana. At Fog Bay all 5 false crawls were associated with turtles attempting to climb the dune. Five turtles (4 at Fog Bay and 1 at Mundabullangana) attempted between 1 and 4 body pits before returning to sea (mean = 2.0; SD = 1.6) without nesting. The mean distance crawled before the initial body pit was constructed was 25.2 m (SD = 18.6; n = 23; range = 6–39 m) at Fog Bay and 24.7 m (SD = 11.2; n = 9; range = 11–39 m) at Mundabullangana which was not statistically different (unpaired t-test: t = 1.17; df = 8; p = 0.36). The number of direction changes of tracks at Fog Bay was 3.8 (SD = 2.6; range = 1–8) before initial body pit, which was significantly less than Mundabullangana where each track had a mean of 4.9 (SD = 1.6; n = 9; range = 1–10) direction changes (unpaired t-test: t = -4.14; df = 8; p = 0.003). Twenty-two (84.6%) of the 26 tracks measured at either site changed direction less than five times before the initial body pit. One turtle track at Mundabullangana changed direction 10 times without obvious signs of disturbance.

Table 2. Results of a four-factor, nested ANOVA for the hen's eggs predation experiment. All F values are shown and p values are shown for all significant variables. Beach was nested within beach type.

Effect	DF	F	p
beach	2,48	0.715	NS
beach type	1,48	3.571	NS
location	1,48	7.0	0.011
treatment	2,48	8.143	<0.001
beach x location	2,48	10.428	<0.001
beach type x location	1,48	0.143	NS
beach x treatment	4,48	0.286	NS
beach type x treatment	2,48	1.0	NS
beach x location x treatment	4,48	4.0	0.007
beach type x location x treatment	2,48	0.143	NS

At Fog Bay there was a mean of 1.1 body pits excavated per successful nest with 16 nests in the first body pit and two in the second. At Mundabullangana a mean of 1.4 body pits per successful nest were made, with six nests in the initial body pit, one nest in the second, and one in the third. Body pit construction appeared to be abandoned because of nest cavity collapse due to loose and/or dry sand when turtles attempted to nest on the dune slope.

Carapace lengths of *N. depressus* at Fog Bay were similar (mean CL = 89.3 cm; SD = 2.1 cm; n = 13) to those at Mundabullangana (mean CL = 88.7 cm; SD = 2.6 cm; n = 241). All 13 turtles encountered at Fog Bay nested at the dune base. At Mundabullangana, 61 turtles nested at the base of the primary dune, 124 nested on its crest, and 56 nested on the secondary dune. There was no significant size difference between turtles that nested at the base of the primary dune and those that nested on its crest (t = -1.36; df = 60; p = 0.179). There was also no significant size difference between turtles that nested on the primary dune and those that nested on the secondary dune (t = -1.09; df = 55; p = 0.281).

Predation rate and the number of clutches laid across beaches and nesting intervals (March–May, June–August, and September–November) for the 1997 and 1998 nesting seasons at Fog Bay (Fig. 1) show the number of nests depredated increased according to nesting density on each beach in each season. Although overall predation rates were higher on the dune base (51.7%) compared to the dune slope (37.8%), they were not significantly different (Mann-Whitney U = 216.00; p = 0.123). Of 5 nests constructed on the dune crest none were depredated.

Of the simulated nests, five "eggs" and six "no eggs" treatments on the dune crest and two of each of the "eggs" and "no eggs" treatments at the dune base were raided and no "flag only" treatments were raided (Table 1). Ten of the simulated nests were raided in the first week although raids continued for one month after the plots were constructed. The four-way nested ANOVA found significantly greater goanna predation of simulated nests on the dune crest (F = 7.0; df = 1,48; p = 0.011; Table 2), which is in contrast to the above finding in natural nests. There was also a significant difference between treatments (F = 8.143; df = 2,48; p < 0.001; Table 2), beach and location (F = 10.429; df = 2,48; p < 0.001; Table 2) and beach, location, and treatment (F = 4.0; df = 4,48; p = 0.007; Table 2). With the exception of the "no eggs" treatment at the dune base of the non-nesting beaches, Tukey's HSD test found that all "eggs" and "no eggs" treatments had significantly greater predation than all "flag only" treatments (all p = 0.025).

DISCUSSION

Natator depressus nested predominantly along the dune base at Fog Bay while at Mundabullangana, as at other major rookeries such as Mon Repos (Limpus, 1971; Bustard et al., 1975), Peak Island (Limpus et al., 1981) and Crab Island (Limpus et al., 1983a), they nested mostly on or beyond the dune crest. Although placement of nests differed, nesting behavior was similar at both sites, apart from afternoon emergence, and more direction changes before initiating a body pit at Mundabullangana. No apparent influence on nest site selection can be implied from these differences, however. The total distance traveled before initiating a body pit was similar at both sites and the higher number of direction changes at Mundabullangana may be reflective of greater hesitancy about where to nest. *Natator depressus* at both sites, nonetheless, made less than five direction changes on most incrawls which is relatively direct compared with other sea turtles (Frazer, 1984; Miller, 1997), agreeing with Bustard et al. (1975) in describing *N. depressus* crawls up the beach as comparatively fast and direct.

Nesting was associated with the high tide at both sites. The size of each nesting turtle did not appear to affect its choice of nesting site. At Fog Bay and Mundabullangana the cues used for timing of emergence, the distance crawled before initiating nesting, and relative directness of crawls were reasonably similar, so it seems most likely that the steeply sloped dunes were responsible for nesting along the dune base at Fog Bay. The total length of false crawls was much longer at Fog Bay than at Mundabullangana and all were associated with attempts to climb the dune.

At Mundabullangana 73% of successful nests were placed beyond the primary dune. Over the 1997 and 1998 nesting seasons 408 of 493 (82.8%) of *N. depressus* nests at Fog Bay were constructed at the dune base (Blamires and Guinea, 2003). Goannas raided approximately 52% of all nests at Fog Bay over the period of this study (Blamires and Guinea, 2003). Goannas rarely raid *N. depressus* nests at Mundabullangana (Prince, 1994). The reason for this is not obvious at the moment. There was no significant difference in the number of nests depredated on the dune slope compared to the dune base at Fog Bay. Five nests were constructed on the dune crest during the study period and were not depredated and nests that hatched had a 100% hatchling emergence success (Blamires and Guinea, 2003), accordingly, this location would appear an ideal place to relocate eggs in order to maximize hatchling output.

Relocation of eggs to the dune crest may be a viable management strategy to prevent goannas raiding nests at Fog Bay if they are incapable of finding nests on the dune crest, rather than merely overlooking them because they were in lower abundance. The hen's egg predation experiment revealed, however, that relocating eggs to the dune crest might not be a solution, as *V. panoptes* raided more simulated nests on the dune crest than the dune base. This may be because the simulated nests were encountered as the lizards moved to and from the beach or, since the eggs were placed randomly and groups of experimental plots were at least 1.0 km distant from each other, goannas may have actively searched the dune crest. Since this phenomenon was not implied for natural nests on the dune crest, it appeared that goannas changed their search habits to account for the changing density distribution of nests, a behavior that has been recognized in raccoons on sea turtle nesting beaches in North America (Hamilton and Standora, 1994).

There was no significant difference in predation of simulated nests between the "no eggs" and "eggs" treatments, both of which goannas raided for up to a month after the experiment began. The "flag only" treatments were never raided. This suggests that visual rather than other cues were used by goannas to identify sand disturbances and thus locate sea turtle nests. Since nesting turtles always create a large sand mound when covering their nests, making exact position of the eggs difficult to locate visually (Bustard, 1972), chemoreception, a strong sense in many varanid lizards (Stamps, 1977), may also be used by goannas to precisely locate sea turtle eggs. Additionally, goannas often raid hatched nests or nests with eggs that have decayed in the nests (Limpus et al., 1983b; Blamires, 1999), implying they may be strongly attracted to odorous nests.

Deterring Goanna Predation at Fog Bay. — Techniques such as nest relocation, smoothing over nests, and chemical deterrents have been effectively used at some American rookeries to protect sea turtle nests from raccoon predation (Stancyk et al., 1980; Hamilton and Standora, 1994; Ratnaswamy et al., 1997). Relocation of nests to other areas of the beach or dunes would be ineffective at preventing goanna predation at Fog Bay, since they locate nests based on areas of disturbed sand. Relocating to a laboratory would require carefully controlled conditions to ensure there was no interference with embryonic development (Blanck and Sawyer, 1981), hatchling sex ratio (Dutton et al., 1985) and natal imprinting, and the release of hatchlings could prove logistically difficult because of the isolation of the area. Relocation onto a non-nesting beach would not increase hatchling production at Fog Bay as the predation experiment found simulated nests were raided as frequently on non-nesting beaches as nesting beaches. Smoothing of the nest surface (Hamilton and Standora, 1994) may not be effective if chemoreception is also used to locate nests. Chemical deterrents need not be ruled out as a possible restraint but require careful experimental testing to ensure they are not detrimental to the eggs, hatchlings, or goannas. Wire screens have been effectively used to deter predators at many rookeries (Wyneken et al., 1988; Ratnaswamy et al., 1997). Trials found that wire screens (90 mm grid size) placed horizontally over nests did not have detrimental affects on hatchling emergence success, while effectively preventing goanna predation at Fog Bay (Blamires and Guinea, 2003), thus appearing an effective deterrent at this rookery. However, wire screens may interfere with the magnetic field around the nest and thus the natal imprinting sense of the hatchlings (Admany et al., 1997). Solid plastic screening may be used in it place of wire, however. An alternative to screens lying horizontally on the sand may be upright cylindrical cages of large enough mesh size to allow hatchlings to escape on emergence. These have proven effective at preventing fox invasion of loggerhead nests at Ningaloo Reef National Park (Prince, unpubl. obs.).

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LITERATURE CITED

ADAMANY, S.L., SALMON, M., AND WITHERINGTON, B.E. 1997. Behavior of sea turtles at an urban beach III. Costs and benefits of nest caging as a management strategy. Florida Scientist 60:239-253.

BLAMIRES, S.J. 1999. Quantifying the impact of predation on sea turtle nests by varanids at Fog Bay. MSc Thesis, Northern Territory University, Darwin.

BLAMIRES, S.J. AND GUINEA, M.L. 1998. Implications of nest site selection on egg predation at the sea turtle rookery at Fog Bay. In: Kennett, R., Webb, A., Duff, G., Guinea, M. L., and Hill, G. J. E. (Eds.). Proceedings of the Marine Turtle Conservation and Management in Northern Australia Workshop. Darwin: Centre for Indigenous and Natural Resources, Centre for Tropical Wetlands Management, pp. 20-24.

BLAMIRES, S.J. AND GUINEA, M.L. 2003. Emergence success of flatback sea turtles (*Natator depressus*) at Fog Bay, Northern Territory, Australia. Chelonian Conservation and Biology 4(3):548-556.

BLAMIRES, S.J., GUINEA, M.L. AND DEVONPORT, C.C. 2001. Using GIS for sea turtle research at the Fog Bay rookery in northern Australia. Marine Turtle Newsletter 92:9-11.

BLANCK, C.E. AND SAWYER, R.H. 1981. Hatchery practices in relation to early embryology of the loggerhead sea turtle, *Caretta caretta* (Linne). Journal of Experimental Marine Biology and Ecology 49:163-177.

BUSTARD, H.R. 1972. Australian Sea Turtles. Their Natural History and Conservation. Sydney: Collins. 220 pp.

BUSTARD, H.R., GREENHAM, P., AND LIMPUS, C. 1975. Nesting behavior of loggerhead and flatback turtles in Queensland, Australia. Proc. K. Ned. Akad. Wet. Ser. C. Biol. Med. Sci. 78(2):111-122.

CHAN, E.H. AND LIEW, H.C. 1989. The Leatherback Turtle; a Malaysian Heritage. Kuala Lumpur: Tropical Press. 49 pp.

DUTTON, P.H., WHITMORE, C.P., AND MROSOVSKY, N. 1985. Masculinisation of leatherback turtle *Dermochelys coriacea* hatchlings from eggs incubated in styrofoam boxes. Biological Conservation 31:249-264.

ECKERT, K.L. 1987. Environmental unpredictability and leatherback sea turtle (*Dermochelys coriacea*) nest loss. Herpetologica 43(3):315-323.

FRAZER, N.B. 1984. A model for assessing mean age-specific fecundity in sea turtle populations. Herpetologica 40(3):281-291.

GUINEA, M.L. 1994. Nesting seasonality of the flatback turtle *Natator depressus* (Garman) at Fog Bay, Northern Territory. In: James, R. (Ed.). Proceedings of the Australian Marine Turtle Conservation Workshop. Canberra: Queensland Department of Environment and Heritage and Australian Nature Conservation Agency, pp. 150-153.

HAMILTON, C.M. AND STANDORA, E.A. 1994. Testing the importance of visual cues in raccoon predation of loggerhead nests. In: Schroeder, B.A. and Whitherington, B.E. (Eds.). Proceedings of the 13th Annual Symposium on Sea Turtle Conservation and Biology. NOAA Tech. Mem. NMFS-SEFSC-341:76.

HAYS, G.C. AND SPEAKMAN, J.R. 1993. Nest placement by loggerhead turtles (*Caretta caretta*). Animal Behavior 45(1):47-53.

HORROCKS, J.A. AND SCOTT, N.M. 1991. Nest site location and nest success in the hawksbill turtle *Eretmochelys imbricata* in Barbados, West Indies. Marine Ecology Progress Series 69:1-8.

KING, D.R. AND GREEN, B. 1999. Goanna: The Biology of Varanid Lizards. UNSW Press, Kensington.

LIMPUS, C.J. 1971. The flatback turtle, *Chelonia depressa* Garman in southeast Queenslan, Australia. Herpetologica 27:431-446.

LIMPUS, C.J., PARMENTER, C.J., PARKER, R., AND FORD, N. 1981. The flatback turtle *Chelonia depressa* in Queensland: the Peak Island rookery. Herpetofauna 13(1):14-18.

LIMPUS, C.J., PARMENTER, C.J., BAKER, V., AND FLEAY, A. 1983a. The Crab Island sea turtle rookery in the north-eastern Gulf of Carpentaria. Australian Wildlife Research 10:173-184.

LIMPUS, C.J., MILLER, J.D., BAKER, V., AND MCLACHLAN, E. 1983b. The hawksbill turtle, *Eretmochelys imbricata* (L.), in north-eastern Australia: the Campbell Island rookery. Australian Wildlife Research 10:185-197.

LIMPUS, C.J., ZELLER, D., KWAN, D., AND MACFARLANE, W. 1989. Sea turtle rookeries in north-western Torres Strait. Australian Wildlife Research 16(5):517-525.

MILLER, J.D. 1997. Reproduction in sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). The Biology of Sea Turtles. Boca Raton, FL: CRC Press, pp. 51-81.

PRINCE, R.I.T. 1994. The flatback turtle (*Natator depressus*) in Western Australia: new information from the Western Australian marine turtle project. In: James, R. (Ed.). Proceedings of the Australian Marine Turtle Conservation Workshop. Gold Coast: Queensland Department of Environment and Heritage, Australian Nature Conservation Agency, pp. 146-149.

RATNASWAMY, M.J., WARREN, R.J., KRAMER, M.T., AND ADAM, M.D. 1997. Comparisons of lethal and nonlethal techniques to reduce raccon depredation on sea turtle nests. Journal of Wildlife Management 61(2):368-376.

SCHROEDER, B. AND MURPHY, S. 1999. Population surveys (ground and aerial) on nesting beaches. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). Research and Management Techniques for the Conservation of Sea Turtles. IUCN/SSC Marine Turtle Specialist Group, Publ. No. 4, pp. 45-55.

SIVASUNDAR, A. AND PRASAD, K.V.D. 1996. Placement and predation of nest in leatherback sea turtles in the Andaman Islands, India. Hamadryad 21:36-42.

SPOTILA, J.R. AND STANDORA, E.A. 1985. Environmental constraints on the thermal energetics of sea turtles. Copeia 1985(3):694-702.

STAMPS, J.A. 1977. Social behavior and spacing patterns in lizards. In: Gans, C. and Tinkle, D.W. (Eds.). Biology of the Reptilia Volume 7. London: Academic Press, pp. 265-334.

STANCYK, S.E., TALBERT, O.R., AND DEAN, J.M. 1980. Nesting activity of the loggerhead turtle *Caretta caretta* in South Carolina, II. Protection of nests from raccoon predation by transplantation. Biological Conservation 18:289-298.

STONEBURNER, D.L. AND RICHARDSON, J.I. 1981. Observations on the role of temperature in loggerhead turtle nest site selection. Copeia 1981(1):238-241.

VANDERLELEY, R. 1996. Nesting ecology of flatback sea turtles at West Alligator Head and Field Island, Kakadu National Park. MSc Thesis, Northern Territory University, Darwin.

WOOD, D.W. AND BJORNDAL, K.A. 2000. Relation of temperature, moisture, salinity, and slope to nest site selection in loggerhead sea turtles. Copeia 2000(1):119-128.

WYNEKEN, J., BURKE, T.J., SALMON, M., AND PEDERSON, D.K. 1988. Egg failure in natural and relocated sea turtle nests. Journal of Herpetology 22(1):88-96.

ZAR, J.H. 1984. Biostatistical Analysis. Englewood Cliffs: Prentice-Hall.

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