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Large-scale investment in the excavation and ‘camouflaging’ phases by nesting leatherback turtles (*Dermochelys coriacea*)

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(Dermochelys coriacea)

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Abstract

Nesting female leatherback turtles, *Dermochelys coriacea* Vandelli, 1761, are ungainly and vulnerable to predation, stranding and physiological stress, dangers encountered repeatedly in a nesting season. Minimising these risks must be balanced against optimising investment in nest site selection, excavation, re-filling, and concealment of their egg clutches. We investigated the relative investment in the different phases of nesting in leatherback turtles by recording the duration of, and respiratory frequency during, each phase. Nest excavation and the final sand scattering (usually termed 'camouflage' or 'disguise') phases were the longest in duration. By combining the relative durations of nesting phases with literature estimates of oxygen consumption, we found that these may be the most expensive phases energetically, sand scattering in particular. Leatherback turtles follow convoluted paths during the sand scattering phase, which were mapped and measured. They disturb large areas (mean $30.3 \pm 11.1 \text{ m}^2$, maximum 57 m^2), the centroids of which were always offset from the nest itself. Interestingly, in none of 26 nestings observed did the centre line of females move over the nest itself. Nesting leatherbacks therefore invest heavily in obscuring the egg clutch, and the pattern of their movements in doing so suggests decoy behaviour.

Keywords

Dermochelys coriacea, leatherback turtles, phase durations, respiration rates, nest disguise, reproductive investment.

Introduction

Sea turtle eggs are unattended after laying and are susceptible to threats that include flooding by the incoming tide, rising water table, exposure by sand erosion, and predation (Welicky et al. 2012). Selection of a suitable nest site, construction and refilling of a protective nest cavity conducive to embryonic development and subsequent escape by hatchlings will all be key factors for reproductive success. Females are themselves vulnerable to hazards such as stranding (Ikaru 2013), predation (Troeng 2000; Troeng et al. 2007), dehydration and other physiological stressors, all of which will increase with the duration of the nesting process. An improved understanding of the investment in time and energy in the various nesting phases could be informative of the selective forces involved in balancing nesting success and maternal survival.

There have been several descriptive accounts of the nesting behaviours of sea turtles (Deraniyagala 1939; Hendrickson 1958; Carr and Ogren 1960; Pritchard 1971; Hailman and Elowson 1992), which have been divided into sequential phases of 'body-pitting', excavation, oviposition, refilling, then a final sand scattering phase usually taken to function to disguise or camouflage the nest. However, there remains little quantitative detail of the nesting process with which to compare different populations or species, and to estimate the relative importance to fitness of different nesting phases. The duration of nesting phases has been measured for several species of sea turtle including the subject of this paper, leatherback turtles *Dermochelys coriacea* Vandelli, 1761 (Eckert and Eckert 1985; Reina et al. 2002).

We report a quantitative analysis of the behaviour and respiration frequency of leatherback turtles during nesting under conditions of minimal disturbance. We included phases not previously distinguished for this species, namely 'prospecting', and we discriminate refilling from sand scattering. Furthermore, we carried out a detailed examination of the movements during sand scattering. This analysis allowed us to estimate the relative temporal and energetic investment in all nesting phases. The findings indicate an unexpected degree of investment in the sand scattering

phase, exceeding even the high relative investment in nest excavation. Our examination of the movements made during the sand scattering phase poses new questions about its function.

Materials and methods

Study area

Fieldwork was carried out at Fishing Pond beach (approximately 10.58° N, 61.02° W) on the East coast of Trinidad. During the study seasons Fishing Pond was one of three protected beaches on the island, it receives high densities of nesting female leatherbacks, and there was no tourist disturbance during our observations. Tagging is carried out on the beach, but none of our observations involved turtles so-disturbed. Beach visits were made on a regular basis from mid-June through to mid-August 2012, 2013 and 2014 during the hours 8 pm– 1 am.

Nesting phases

Discrimination of nesting behavioural phases was modified from previous publications (Hendrickson 1958; Carr and Ogren 1959, 1960; Pritchard 1971; see also Burns et al. 2015). Eight phases were defined and will be referred to as follows: 1 - approach (movement from surf to upper beach); 2 - prospecting (movement within the nesting area of the upper beach to select a nest site, sometimes involving beginning of body-pitting but then rejection of site and movement elsewhere); 3 - body-pitting (preparation of the nest site for excavation); 4 - excavation of the nest chamber; 5 – egg laying; 6 - refilling the nest cavity; 7 - sand scattering (usually termed nest ‘camouflaging’ or ‘disguising’ in the literature); 8 - return to the sea (see Supplementary Data Table S1 for full definitions and descriptions used). The first and last of these are clearly dependent on tide and distance to the sea, but they nevertheless involve physiological effort. We use the term ‘sand scattering’ as less presumptive than the usual terms.

Respiratory frequency

An observer positioned to the side of a turtle's head used the sound of exhalation/inhalation and observed movements of the turtle's head and mouth to record each breath. Breathing intervals presented are from the beginning of an exhalation to the beginning of the next. Dim red light was used to illuminate the turtle's head when ambient light was insufficient. Stopwatch readings were taken at the time of each breath.

Estimated oxygen consumption

Oxygen consumption during each phase of nesting was estimated using published values obtained during different beach activities (Paladino et al. 1990, 1996) combined with our recorded values for relative temporal investment in each nesting phase (using values only from individuals for which all nesting phases were timed, $n = 21$).

Sand scattering pathways and area disturbed

Markers were placed to indicate nest positions and to delineate the edges of visibly disturbed areas of sand and path of the turtle. Sketches taken during sand scattering were later scaled using tape measurements taken after a turtle had returned to the sea. Methods of sketching differed between years; in 2012 ($n = 9$), paths were marked using a continuous curved line; in 2014 ($n = 17$), paths were marked with straight lines between each position at which the turtle stopped to scatter sand. Scaled drawings were scanned and image files were analysed using ImageJ 1.46 software (<http://imagej.nih.gov/ij/>) to determine areas, distances, and the centroid of the disturbed area.

Data analysis and presentation

Statistical procedures were carried out using R software (<http://www.r-project.org>) unless otherwise stated. Repeated measures analysis of variance (ANOVA, 'aov' function) were used to examine differences in the duration of different phases of nesting. Behavioural phases were set as categorical fixed effects and individual as a random effect. Post hoc tests were performed in the form of

pairwise comparisons with a Tukey adjustment (lsmeans package), to compare between phases. The same method was also used to examine variation in intervals between breaths for different nesting phases. All graphing and curve fitting was carried out using Microcal ORIGIN software.

Results

Nesting phase durations

Durations of nesting phases were recorded for a total of 34 individuals, for 21 of which the entire nesting process was observed. The mean (\pm SD) time for the entire nesting process was 100.7 ± 12.8 mins (range=72.5 to 124.5 mins, $n=21$), of which excavation and sand scattering stood out as being the longest phases (ANOVA, $p < 0.0001$, $df = 139$ and $n = 21$ for each in pairwise comparison with remaining phases) with means of 23.2 ± 7.3 and 28.1 ± 7.8 mins, respectively (Figure 1). On average, they together comprised over half of the overall nesting duration, with sand scattering found to be significantly longer in duration than excavation (ANOVA, $p = 0.0077$, $df = 139$, $n = 21$). Nest site selection behaviour (prospecting) durations varied considerably between individuals arriving in the nesting zones of the beach, ranging from 0 to 25 minutes ($n=22$) and constituting 0 to 17.0% of total nesting time ($n=21$); only the excavation and sand scattering phases had a greater variance in duration and proportion of the overall nesting period.

Respiratory frequency

Breathing frequency during each nesting phase was recorded for six individuals, all of which showed an irregular pattern, with continuous fluctuations in the interval between breaths throughout the nesting process (see Figure 2A for a typical case and Figure S1A to F for all the observations made). There were no statistically significant differences in the intervals between breaths during the approach, prospecting, body pitting, excavation, sand scattering, and return to sea phases (ANOVA,

$p > 0.05$ for all pairwise comparisons, $n = 6$ individuals, $df = 25$). The laying phase exhibited by far the lowest breathing frequency (ANOVA, $p < 0.02$ for all pairwise comparisons, $n = 6$, $df = 25$) with a mean of 2.3 breaths per minute (range = 1.6 - 3.1 breaths/min) (Figure 2B).

Estimated oxygen consumption

Assuming published measurements for oxygen consumption by leatherbacks on land while at rest or exercising are reasonable relative estimates of physiological effort (Paladino et al. 1990, 1996), comparative estimates of oxygen consumption between nesting behavioural phases again emphasised the high relative investment by nesting females in the excavation and sand scattering phases (Table 1).

Sand scattering pathways and disturbed area

Paths travelled during sand scattering, and the size of the disturbed area, were mapped for 26 females (Figure S2). This phase involves periodic movements between stops at which turtles scatter sand and then move on often in a different direction to a new sand scattering station. See Table 2 for total distances travelled, areas disturbed, and displacements between the centroid of disturbed areas and nest positions. Notably, no individual was found to circumnavigate or directly cross over the nest itself, the nest position was always considerably offset from the centroid of the disturbed area (Table 2, Figure S2), and in only three cases did a female closely approach the nest. As detailed in Table 2, disturbed areas were up to 57 m² in extent, and the distance between the centroid and the nest was up to 5 m.

Discussion

In this study we investigated the relative temporal and physiological commitments by leatherback turtles in the different phases of nesting. We found that the nest excavation and the sand scattering phases are longest in duration (Figure 1) and potentially the most energetically expensive (Table 1). A high degree of investment into the sand-scattering phase is clear, and the more surprising given

that the females may be physiologically stressed at the end of a prolonged sojourn on land yet remain active rather than return promptly to the sea. Our mapping of movements during sand scattering is to our knowledge the first time this has been done for any species of sea turtle, and revealed a counter-intuitive pattern of movements.

Excavation and sand scattering phases together comprised on average more than half the total time on land. Large scale investment is perhaps unsurprising given the need to excavate a cavity that will be the environment in which eggs must be safe to develop, and from which hatchlings must escape. But that an equivalent or even greater proportion of the time is spent scattering sand after the nest cavity has been re-filled is surprising. With regard to the refilling and sand scattering phases, our separation of them proved crucial to appreciating their separate contributions to the overall nesting effort. A comparison between our findings and those of other studies is given in Table S2.

We found no significant differences in the respiratory frequency between nesting phases, with the exception of laying. A potential limitation to our technique is that, while there may be no change in respiratory frequency, the volume of air inhaled in each breath may vary, which has been demonstrated in leatherbacks during nesting (Lutcavage et al. 1990; Paladino et al. 1996; Cook and Forest 2005). A further consideration is the potential for a degree of anaerobic metabolism that may influence the use of respiratory frequency as a proxy measure of energy expenditure. This could potentially lead to an underestimate of energy expenditure in phases in which it occurs, followed by an overestimate in subsequent phases when increased ventilation may be required to compensate. However, the results of a previous study examining respiratory physiology suggest anaerobic respiration is not heavily utilised during nesting (Paladino et al. 1996). If one accepts previously published oxygen consumption rates of leatherbacks (Paladino et al. 1990, 1996), measured during moving on the beach, excavating, and laying, as being workable approximations for undisturbed turtles, then the relative scale of investment in sand scattering is further emphasised (Table 1).

No previous studies have recorded breathing rates continuously throughout nesting of a sea turtle, though a significant drop in the respiratory frequency during laying has been noted before. Lutcavage et al. (1990), reported a mean respiratory frequency of 2.3 breaths/minute, and Cook and Forrest (2005) reported the rate of production of exhale/inhale sounds during the laying phase as being on average just below two breaths/minute. Interestingly, Cook and Forrest (2005) noted that although the rate of exhale/inhale sounds remained fairly constant between the 'covering' (refilling) and 'camouflaging' (sand scattering) phases, the duration of these sounds significantly increased. This suggests that in addition to the rate, the duration of breathing events could be important to record when using non-contact methods of measuring respiration frequency.

The sand scattering phase is variously termed 'camouflaging' and 'disguise' in the literature. While these terms reflect reasonable deductions, there is little if any formal evidence that it performs this function. Other than simply disguising the position of the nest against visual location by predators, it may also act to disperse any associated odour from the mother, the eggs or cloacal fluids as further defence against detection by nest predators or parasites. In our mapping of the paths taken by females during sand scattering we found that the females move up to 9m from the nest site and disturb an area of up to 57 m² (Table 2). Perhaps more significantly, the area disturbed was never centred on the nest hole, the centroids being significantly displaced from the nest, and the females rarely approached the nest itself (Table 2; Figure S2). This could be due to an inability to navigate circumferentially around the nest, but it would be consistent with decoy behaviour to distract predators from localising the nest by simple centring of a circular disturbed area either visually, tactilely, or by smell. However, offsetting of the disturbed area would not be consistent with the hypothesis that sand scattering contributes to optimising the temperature and moisture levels of the sand in the immediate proximity of the nest (Miller 1997).

No previous studies have discriminated or measured the prospecting stage of nesting for leatherbacks, yet the choice of nest site is crucial to reproductive success (Caut et al. 2006). The

literature refers little, if at all, to this behaviour; it is variously disregarded (Carr and Ogren 1959), not referred to (Pritchard 1971; Reina et al. 2002), or noted but not distinguished from other phases (Eckert and Eckert 1985). We observed, for instance, that initial nesting attempts were abandoned because of nearby surface obstructions, or those encountered during digging, prolonging site selection and time on land, although abandonments were often observed with no obvious impediment (to a human). Ensuring safety of the clutch from disturbance, flooding, and provision of a suitable nest environment, are clearly crucial, and the incubation temperatures of clutches determines the gender of hatchlings in sea turtles (Standora and Spotila 1985). The need for prospecting is therefore likely to vary considerably between nesting beaches that differ in topography and/or sand quality, both of which may change during a nesting season.

Our findings have both evolutionary and ecological implications. Quantitative analysis of the leatherback nesting process should allow direct comparisons with other populations or species of sea turtle. For instance, how does allocation of resources to nesting phases vary between populations or species? What are the selective forces that govern this variation? Could the absolute and relative durations of nesting phases be affected by disturbance, such as tourist activity or predator presence around a nesting female (as shown for both loggerhead *Caretta caretta* L., 1758 (Johnson et al. 1996) and green turtles, *Chelonia mydas* L., 1758 (Mendonça et al. 2010)), or the proximity of noise, lights, and buildings? Are phase durations density-dependent - that is, if a beach is heavily nested, resulting in interactions between turtles, will the relative lengths of phases alter? For the moment, examination of the details of nesting by marine turtles, and how they vary between and within species, could inform on the selective forces that have shaped the evolution of instinctive nesting behaviours. In particular, the importance of disguising the nest site, and what cues for predators or parasites they may be attempting to disrupt.

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Table 1. Estimation of oxygen consumption of the leatherback turtle, *Dermochelys coriacea* by nesting phase^a.

Phase	% of total nesting duration	VO ₂ (ml O ₂ /kg/min)	O ₂ Use (ml O ₂ /kg)	Proportion of overall O ₂ use (%)
Approach	7.4	2.6	19.1	7.3
Prospecting	7.1	2.87	20.3	7.8
Body pitting	6.1	2.87	17.7	6.7
Excavation	23.5	2.87	67.3	25.9
Laying	11.4	0.87	9.9	3.8
Refilling	10.9	2.87	31.2	11.9
Sand scattering	28.9	2.87	82.8	31.7
Return to sea	5.0	2.6	12.9	4.9
Total			261.2	

^aCalculated using VO₂ values from Paladino et al. (1996) for egg laying (0.87 ml O₂/kg/min) and exercising (2.87 ml O₂/kg/min), and values from Reina et al. (2002) (which they quote as calculated from Paladino et al. (1990)) for walking (2.6 ml O₂/kg/min). We make the assumption here that these literature values for exercising approximate the active phases of the nesting process (prospecting, body pitting, excavation, refilling and sand scattering). The proportions of the total nesting duration taken up by each phase is based upon values from individuals for which durations of all nesting phases were known ($n = 21$). Data from 2012 and 2013 seasons, values displayed have been rounded to one decimal place.

Table 2. Distance parameters in the sand scattering phase of the leatherback turtle, *Dermochelys coriacea*, data gathered during the 2012 and 2014 seasons ($n = 26$; SD = standard deviation), see Figures S2A to Z for the sand scattering movement maps from which values were extracted.

Parameter	Mean \pm SD	Range
Total distance travelled (m)	13.5 \pm 3.9	7.2 - 23.7
Total area of disturbed sand (m ²)	30.3 \pm 11.1	13 - 57.4
Nest distance from centroid of disturbed area (m)	3.1 \pm 0.9	1.7 - 4.9
Maximum distance moved from nest site (m)	5.9 \pm 1.8	3.6 - 9.7

Figure 1. Duration of nesting phases of leatherback turtles, *Dermochelys coriacea*. Box and whisker plots of measurements of complete phases observed (mean (*), median (horizontal line in the boxes), box boundaries are 25 and 75 percentiles (Q1 and Q3, respectively), and range (bars)). Sample sizes as indicated above plot for each phase. See Materials and Methods and ESM Table S2 for detailed descriptions of the phases. Data from 2012 and 2013 seasons.

Figure 2. Changes in breathing frequency during the nesting process of leatherback turtles, *Dermochelys coriacea*. (A) Typical data from a single nesting. See Supplementary Data Figure S1A to F for all the nestings recorded. (B) Box and whisker plots of measurements accumulated over several nestings – graphing details as for Figure 1. Sample sizes as indicated. Data from 2012 and 2013 seasons. See Materials and Methods and Table S1 for detailed description of the phases.

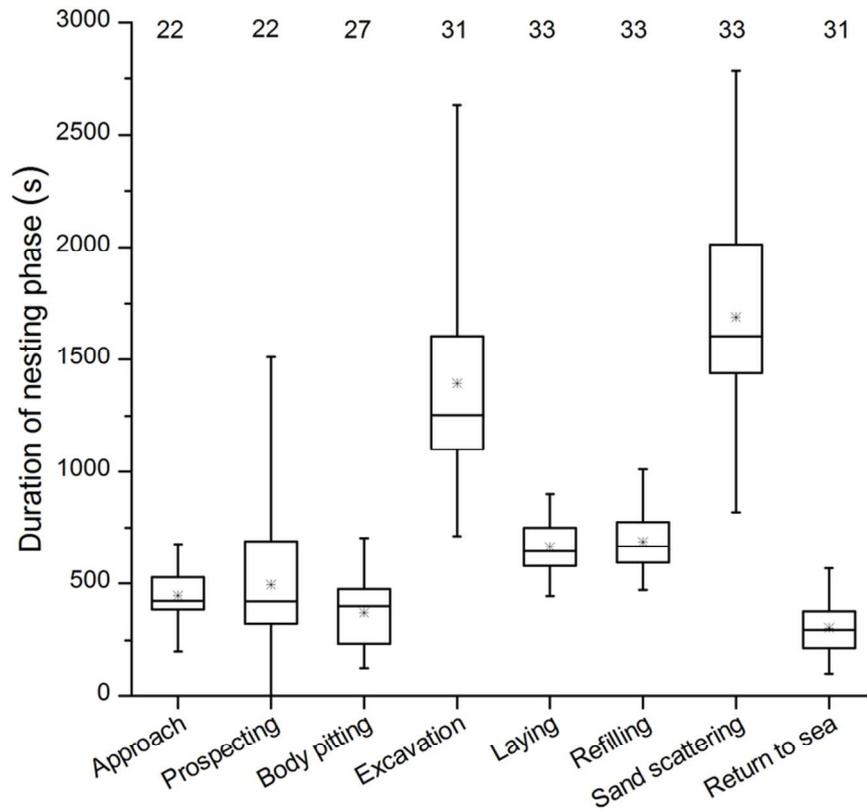


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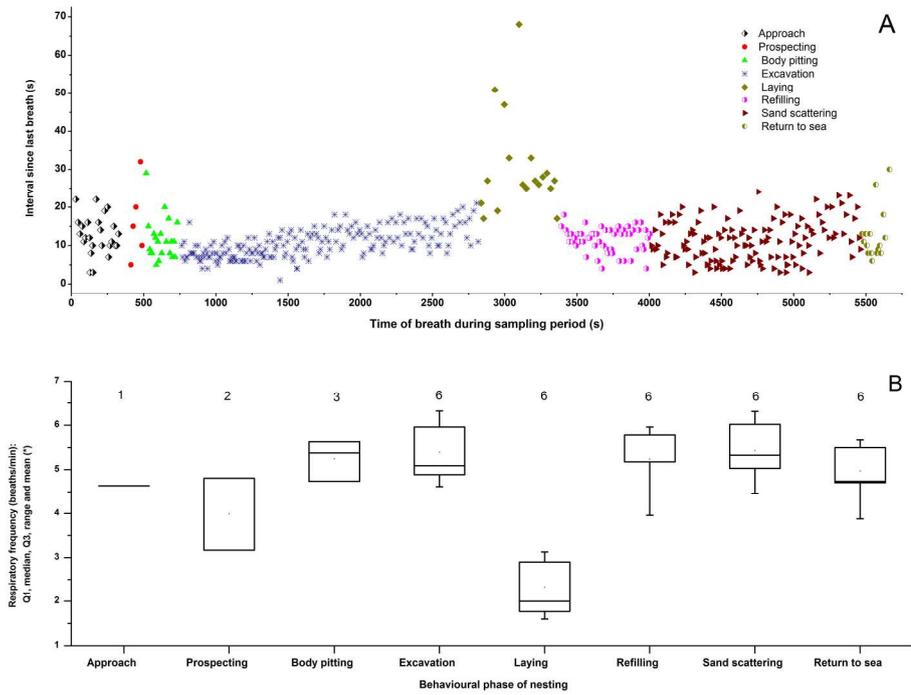


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