The importance of sand albedo for the thermal conditions on sea turtle nesting beaches

G. C. Hays, J. S. Ashworth, M. J. Barnsley, A. C. Broderick, D. R. Emery, B. J. Godley, A. Henwood and E. L. Jones

Hays, G. C., Ashworth, J. S., Barnsley, M. J., Broderick, A. C., Emery, D. R., Godley, B. J., Henwood, A. and Jones, E. L. 2001. The importance of sand albedo for the thermal conditions on sea turtle nesting beaches. – Oikos 93: 87–94.

At Ascension Island and Cyprus, major nesting areas for green turtles (*Chelonia mydas*) in the Atlantic and Mediterranean, respectively, visual inspection shows some beaches are light in colour while others are darker. We objectively measured the albedo of the sand on different beaches, i.e. the percentage of the incident solar radiation that was reflected from the sand surface. At sites where albedo was recorded, we also measured the temperature of the sand at nest depths. At both rookeries, the sand temperature was markedly higher on darker beaches due to greater absorption of the incident solar radiation over the diurnal cycle. Temperature loggers buried at nest depths revealed seasonal changes in temperature on both islands, but showed that the lowest temperatures found on the darker beaches rarely dropped below the highest temperatures on the lighter beaches. Sea turtles exhibit temperature-dependent sex determination. Since sand albedo is a major avenue for the production of a range of incubation temperatures on both islands, it will also have profound implications for hatchling sex ratios. In comparison with both Ascension Island and Cyprus, for samples collected from sea turtle rookeries around the world there was an even greater range in sand albedo values. This suggests that sand albedo, a factor that has previously received little consideration, will have profound implications for nest temperatures, and hence hatchling sex ratios, for other populations and species.

G. C. Hays, J. S. Ashworth, A. C. Broderick, B. J. Godley, A. Henwood and E. L. Jones, School of Biological Sciences, Univ. of Wales Swansea, Singleton Park, Swansea, UK SA2 8PP (g.hays@swan.ac.uk). – M. J. Barnsley, Dept of Geography, Univ. of Wales Swansea, Singleton Park, Swansea, UK SA2 8PP. – D. R. Emery, Dept of Geography, NERC Equipment Pool for Field Spectroscopy, Univ. of Southampton, Southampton, UK SO17 1BJ.

Since its discovery in reptiles over 25 years ago (Pieau 1972), the phenomenon of temperature-dependent sex determination (TSD) has generated considerable interest amongst behavioural, physiological and evolutionary ecologists. While there continues to be heated debate about its functional significance and how this phenomenon may have evolved (e.g. Shine 1999), the existence of TSD in a wide variety of turtles, lizards and snakes is now undisputed (Janzen and Paukstis 1991, Ciofi and Swingland 1997). Consequently there is huge interest in, for example, how species exhibiting

TSD currently manage to produce offspring of both sexes, how populations might respond to global warming and how deleterious responses might be mitigated (e.g. Davenport 1997, Rhen and Lang 1998, Godfrey et al. 1999). This interest is particularly acute for sea turtles since most species are already endangered.

For sea turtles, the sex of hatchlings is determined by the temperature during the middle third of incubation with females being produced at higher incubation temperatures and vice versa. Although sea turtles nest over a broad latitudinal range (between approximately 30°S

and 40°N), and different species nest at markedly different depths, for all species and populations so far examined the incubation temperature marking the switch from predominantly male to predominantly female offspring (termed the pivotal temperature) has always been found to be close to 29°C (Ackerman 1997). Consequently the factors that produce a range of incubation temperatures around 29°C are vital for ensuring the survival of populations. While a number of population specific factors have been identified in causing inter-nest thermal variations, a general understanding of the key factors that dictate nest temperatures on a global scale has remained elusive. For example, for loggerhead turtles nesting on the east coast of the USA, seasonal changes in sand temperature occur so that mainly males are produced at the start and end of the nesting season and females during the interim (Mrosovsky et al. 1984); for green turtles nesting in Costa Rica the incubation temperature is profoundly influenced by whether the nest is shaded by vegetation (Morreale et al. 1982); while for the green turtle rookery at Ascension Island there are large inter-beach thermal variations caused by differences in sand albedo (i.e. the percentage of incident solar radiation reflected by the sand) (Hays et al. 1995a) and these variations are maintained both within and between seasons (Hays et al. 1999). Given this previously reported importance of sand albedo at Ascension Island, here we set out to assess the wider importance of this parameter. We first critically examine an existing simple and low cost method of measuring sand albedo; next we consider whether the links between sand albedo and temperature reported previously at Ascension Island are found elsewhere; finally we consider how the sand albedo on sea turtle nesting beaches varies globally and hence its potential ecological importance for sea turtles in general.

Methods

Field technique for measuring the albedo and temperature of the sand

The term albedo is generally used to describe the fraction of incident solar radiation reflected from a surface. For a surface in which transmission of radiation can be considered as zero (e.g. sand on a beach), the complementary value to the albedo is the absorptance, i.e. the fraction of the incident solar radiation that is absorbed by the sand. In other words, darker surfaces will have a lower albedo and a higher absorptance, while lighter coloured surfaces will have a higher albedo and lower absorptance. It is common practice to express both albedo and absorptance as percentages, i.e. absorptance = 100 − albedo.

On both Ascension Island (7°57′ S, 14°22′ W) and Cyprus (35°33′ N, 33°47′ E) we used the following technique to measure the sand albedo (ρ) during the respective nesting seasons in 1999 on each island. Under clear sunny skies, we used a standard photographic lightmeter (Sekonic Dual Spot F L-778, Tokyo, Japan) to measure reflected solar radiation at visible wavelengths from the sand (L_S) and then from a photographic grey card of known albedo (18%) under the same illumination conditions (L_G). We made five consecutive pairs of readings (sand then grey card) from which means were calculated. Before measurements the sand surface was smoothed. Measurements were always made in conditions of zero cloud cover, in order to remove the possibility of the incident radiation changing between sand and grey card measurements. The light meter was hand held in a vertical position 25 cm above the sand and pointing downwards, with no shadows being cast on the measurement area. In these ways conditions were standardised between sand and grey card measurements.

Since the spectral response curve of the Sekonic L-778 (supplied by the manufacturer) shows peak sensitivity around 550 nm and a spectral range from about 350 nm to 800 nm, readings made with this instrument only refer to visible wavelengths. A measure of the albedo of the sand within visible wavelengths (350–800 nm) was thus calculated as:

$$\rho_{350-800} = (L_S/L_G) \times 18\%$$

From this albedo value, the absorptance of incident solar radiation (α) within visible wavelengths, was then calculated as:

$$\alpha_{350-800\text{field}}(\%) = 100 - \rho_{350-800}$$

At sites where $\alpha_{350-800\text{field}}$ was measured we dug down to a depth of 75 cm (which lies within the normal range of green turtle nest depths on each island) and measured the sand temperature with a temperature probe (Checktemp, Hanna Instruments, Leighton Buzzard, UK). Measurements of $\alpha_{350-800\text{field}}$ and temperature were made between 24 and 28 May 1999 at Ascension Island and throughout the 1999 nesting season on Cyprus. In addition, on light and dark beaches on both islands we placed temperature loggers (Tinytalk II, Gemini data loggers, Chichester, UK) at 75 cm and monitored the temperature throughout the 1998/1999 nesting season at Ascension and the 1999 nesting season at Cyprus. On Ascension Island there were three control sites per beach while on Cyprus there was one per beach. The absolute accuracy of these loggers was established by cross-calibration in controlled conditions against NAMAS certified mercury thermometers (Hays et al. 1999).

To measure the extent of metabolic heating (i.e. the warming of the nest environment by the developing embryos), loggers were placed in nests on both islands and the in-nest temperature recorded throughout incubation (i.e. until hatchling tracks were observed to emerge from nests). In this way we quantified the warming that occurred between the start and middle third of incubation. From this value, we subtracted the seasonal change in sand temperature recorded at the control site(s) on that particular beach over the corresponding period, with the resulting value being the amount of metabolic heating.

Validation of field technique for measuring sand albedo

Photographic lightmeters, such as the Sekonic L-778, only measure reflectance in the visible part of the spectrum, i.e. reflectance in near and short-wave infra-red wavelengths is not measured. However, these wavelengths are potentially important in heating the sand. We therefore validated our field technique for measuring sand albedo, by comparison of this technique against a broad-band spectroradiometer which measures throughout the visible and infra-red wavelengths. The steps in this validation were first to use our photographic light meter to measure the $\alpha_{350-800}$field. Second, we collected surface sand samples from these measurement sites. Third, we brought these samples back to our laboratory in Swansea, and 2–6 months after they had been collected we again used the photographic lightmeter to measure α using the same protocol as in the field except that measurements were made in the laboratory under overhead electric lights. We termed these laboratory values the $\alpha_{350-800lab}$. Fourth, using established protocols (Milton et al. 1995, 1997) we measured the broad-band absorption of the sand samples using a spectroradiometer (FieldSpec FR, Analytical Spectral Devices, Boulder, CO, USA) which measures the reflectance in 1-nm increments between 350 and 2500 nm. These measurements were made at the Natural Environment Research Council's Equipment Pool for Field Spectroscopy, a centre established specifically for spectral reflectance measurements (including albedo) and whose instruments and facilities are calibrated against National Physical Laboratory standards. Here laboratory measurements were made under the most exacting conditions possible. Measurements were made in a blackened room to prevent any internal reflection of light. The only light source was a single tungsten-halogen lamp (with a spectral signal approximating that of the Sun) positioned at an angle of 45° adjacent to the sample. The spectroradiometer was held in a clamp vertically above either a Petri dish containing a sand sample or a white panel of known albedo (this reference panel was made of Spectralon (Labsphere Inc, NH, USA) an acknowledged international standard). The measurement distance from the spectroradiometer to either the sand surface or the reference panel was always the same (25 cm) with the measurement angle of the spectroradiometer being 8°. The sand surface was smoothed before measurements. Five pairs of readings (sand and then reference panel) were made, from which means were calculated. These measurements represent the most exacting albedo measurements possible using state of the art equipment and hence provide the definitive values against which to compare our results obtained with simple photographic lightmeters and less exacting field protocols.

The actual amount of incident radiation absorbed by sand is a product of both its absorptance at different wavelengths, α_λ, and the incident solar radiation at that wavelength, E_λ. Thus, at certain wavelengths α_λ may be very large, but, if E_λ at that wavelength is small, then the potential impact in sand heating will be minimal. We calculated the relative importance of different wavelengths in the incident radiation by using Planck's law. This approach will only provide an approximation to the incident radiation, since atmospheric gases, particularly water vapour, will preferentially absorb certain wavelengths (e.g. Vermote et al. 1997). Nevertheless Planck's law describes the main patterns in the incident spectrum at the Earth's surface, with a peak in the visible wavelengths, and so suffices for our purposes. To calculate the overall percentage of incident radiation between 350 and 2500 nm that was absorbed by the different sand samples we therefore first calculated E_λ in each 1-nm step over this range and then multiplied these values by α_λ for the corresponding wavelengths and summed their product, i.e. absorbed radiation $= \Sigma_{\lambda300}^{\lambda2500} (E_\lambda \times \alpha_\lambda)$. We defined this product as the $\alpha_{350-2500}$.

Sand samples from other nesting areas

To provide an indication of the global range in the albedo values for nesting beaches, we obtained sand samples from rookeries around the world, namely Australia, Costa Rica (two beaches), Bangladesh, Bahamas, Greece (two beaches), India, Israel (four beaches), Japan, Malaysia, Mexico (three beaches), Puerto Rico, the USA (Alabama, Florida (three beaches) and Georgia) and the US Virgin Islands. These samples were kindly provided by participants at the 19th Annual Symposium on Sea Turtle Biology and Conservation, following a request for individuals to donate samples from their particular study beaches. For each of these samples we measured $\alpha_{350-800lab}$.

Nest depths

To critically assess whether nesting depth was adjusted depending on the albedo of the sand we used nest depth data collected in 1992 (Hays et al. 1993). For two beaches of contrasting albedo on Ascension Island, Long Beach and NE Bay Beach, we used a semi-rigid tape to measure the depth (1) from the sand surface to the bottom of the egg chamber and (2) from the sand surface to the top-most egg. These measurements were made at the time of egg-laying. During these measurements the beach surface was defined by placing a 3-m wooden ruler over the nest with the ruler resting on the undisturbed sand surface on either side.

Results

Within-beach variation in albedo

On Ascension Island we measured $\alpha_{350-800field}$ at three sites on each of the three beaches which contained the highest nesting activity: Long Beach, North East Bay Beach and South West Bay Beach. Measurements were made in the zone of maximum nesting density at three equally spaced points along the beach. Individual beaches at Ascension Island look uniform in coloration and this impression was supported by the $\alpha_{350-800field}$ measurements which revealed that intra-beach variations did not obscure inter-beach variations, with the measurements at the separate sites on each beach: Long Beach 65%, 65% and 63%; NE Bay Beach 83%, 80% and 75%, and South West Bay beach 69%, 69% and 63%. At Cyprus, albedo measurements were again made in the zone of maximum nesting activity on each beach, with the number of albedo measurement sites being scaled according to the nesting density on each beach. So for seven beaches, $\alpha_{350-800field}$ was only measured at one site per beach, but for the remaining 35 beaches, $\alpha_{350-800field}$ was measured at between two and 39 sites. The mean $\alpha_{350-800field}$ values for different beaches at Cyprus varied from 69% to 91% and again this between beach variation was not obscured by within-beach variation, with the mean SD for within beach measurements being only 2%.

Validation of field protocols

All three measures of absorptance ($\alpha_{350-800field}$, $\alpha_{350-800lab}$ and $\alpha_{350-2500}$) were made for sand samples collected from 13 beaches on Cyprus and 23 beaches on Ascension Island. The values for $\alpha_{350-800field}$ and $\alpha_{350-800lab}$ were highly correlated, although, on average, the values for $\alpha_{350-800field}$ were 2.3% lower than the values for $\alpha_{350-800lab}$, a difference which, despite being small in absolute terms, was significant (paired t-test,

$n = 36$, $t = 3.43$, $P = 0.002$) (Fig. 1a). Both the values for $\alpha_{350-800field}$ and $\alpha_{350-800lab}$ were much larger than those for $\alpha_{350-2500}$, the differences averaging 11.0% and 13.3%, respectively, although these measures were all highly correlated (Fig. 1b).

Albedo versus sand temperature

Temperature at nest depths and $\alpha_{350-800field}$ were recorded for a total of 24 sites on 18 different beaches on Ascension Island and at 55 sites on 21 beaches on Cyprus. At both islands, the sand temperature at nest depths increased as the $\alpha_{350-800field}$ value increased, i.e. darker beaches were warmer, as one might expect (Fig. 2a, b). To provide an indication of the thermal conditions which would occur in the middle third of incubation within nests on beaches of contrasting albedo, we added the mean metabolic heating measured on each island ($n = 32$ loggers placed in 32 nests on Ascension Island; mean metabolic heating = 1.0°C, SD = 0.7; $n = 17$ loggers placed in 11 nests on Cyprus; mean metabolic heating = 0.73°C, SD = 0.23, $n = 11$ nests) to
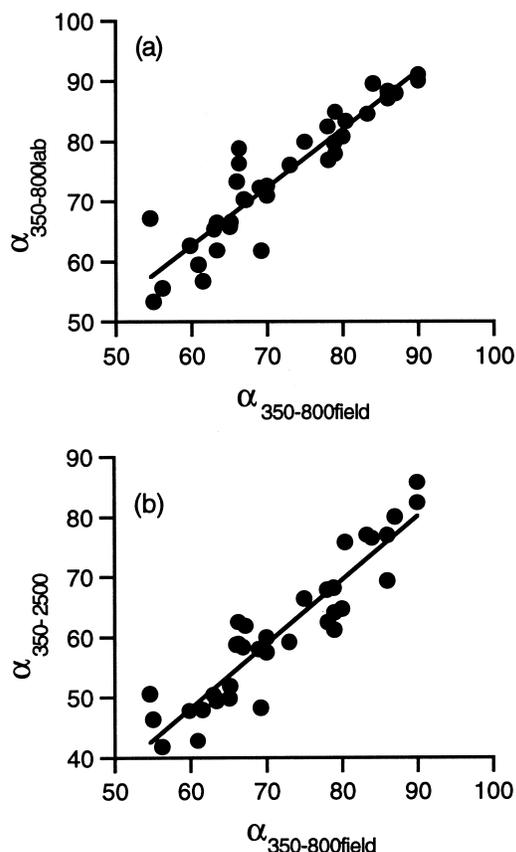

Fig. 1. The relationships between (a) $\alpha_{350-800field}$ and $\alpha_{350-800lab}$; (b) $\alpha_{350-800field}$ and $\alpha_{350-2500}$. In both cases, correlation coefficients were very high ($r^2 = 0.86$ in both cases).

Fig. 2. (a and b) The relationships between the sand temperature at nest depths and the absorption of incident solar radiation by the sand ($\alpha_{350-800field}$) for sites on Ascension Island and Cyprus, respectively. Points represent mean values for individual beaches. $F_{1,16} = 70.7$, $P < 0.001$, $r^2 = 0.82$ and $F_{1,19} = 69.8$, $P < 0.001$, $r^2 = 0.79$, respectively. (c and d) For a dark (warm) and a light (cool) beach on each island, the seasonal variation in the in-nest temperatures during the middle third of incubation, determined by adding the mean extent of metabolic heating on each island to the temperatures measured at control sites throughout the nesting season. x = the mean $\alpha_{350-800field}$ value for the respective beaches. The dark and light beaches on Ascension Island were NE Bay Beach and Long Beach, respectively, where nest depths were also measured. The nesting season lasts from approximately December to May on Ascension Island and from June to August on Cyprus, with peaks in nesting in February–March and June–July, respectively.
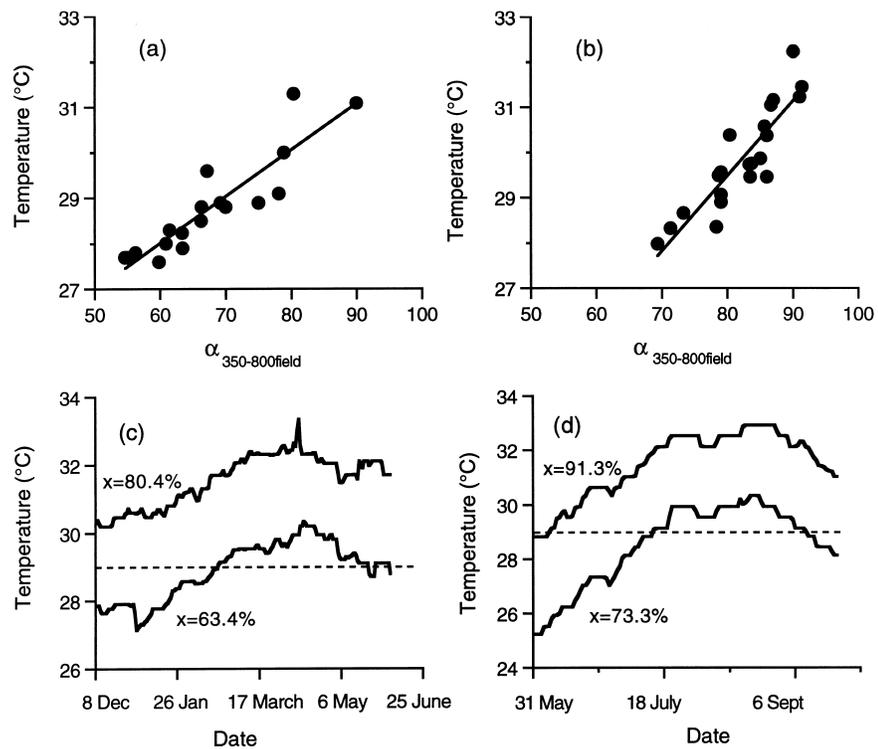
the temperatures recorded at control sites on different beaches. This analysis showed that inter-beach thermal variations were maintained throughout the nesting season on both islands and were of sufficient magnitude that the overlap in temperature between dark and light beaches was minimal (Fig. 2c, d), i.e. the highest temperatures recorded on the lightest beaches rarely reached the lowest temperatures recorded on darkest beaches. Most importantly, whether temperatures lay above or below 29°C was strongly dependent on the albedo of the beach, with cooler male-producing temperatures generally only being found on the lighter coloured beaches.

Albedo measurements for samples from around the world

For samples from around the world, $\alpha_{350-800lab} - 2.3\%$ were calculated, to take account of the measured differences between the field and laboratory measurements. The range in sand albedos measured from the different nesting beaches around the world, was comparable to that found at Ascension Island and Cyprus (Fig. 3) with the darkest beach being found in Costa Rica ($\alpha_{350-800lab} - 2.3 = 89.6\%$) and the lightest beach being found in the Bahamas ($\alpha_{350-800lab} - 2.3 = 44.4\%$).

Nest depth versus albedo

Between the dark and light beaches on Ascension Island (NE Bay Beach and Long Beach respectively) there was no significant difference between either the mean depth from sand surface to the bottom of the egg chamber (NE Bay Beach: mean = 93.3 cm, SD = 11.5, $n = 18$; Long Beach: mean = 89.9 cm, $n = 21$; $t_{35} = 0.97$, $P > 0.05$) or the mean depth from the sand surface to the top-most egg (NE Bay Beach: mean = 67.5 cm, SD = 13.4, $n = 17$; Long Beach: mean = 60.8 cm, SD = 14.5, $n = 22$; $t_{35} = 1.5$, $P > 0.05$).

Discussion

In order to assess the importance of sand albedo for sea turtles, it is clearly important to develop a technique for measuring this parameter. In order to have wide applicability, any such technique must ideally be accurate, simple and cheap. Reflectance measurements taken with a photographic lightmeter referenced to a standard grey card potentially provides such a technique and so this is the approach we have used in the field. However a limitation of simple lightmeters is that they generally only measure reflectance in the visible spectrum while the incident spectrum will also be composed of other

wavelengths (e.g. infra-red radiation) that may also be important in sand heating. Instruments for measuring across a wider spectrum (visible light + infra-red) are vastly more expensive and used for dedicated spectroscopy studies which are likely to be beyond the feasibility of most sea turtle projects (Milton et al. 1995, 1997). It is therefore important to ascertain that our field technique for measuring the percentage of the incident energy absorbed by the sand is reliable. In this context, we would not expect $\alpha_{350-800\text{field}}$ and $\alpha_{350-2500}$ values to be the same in absolute terms, since they are
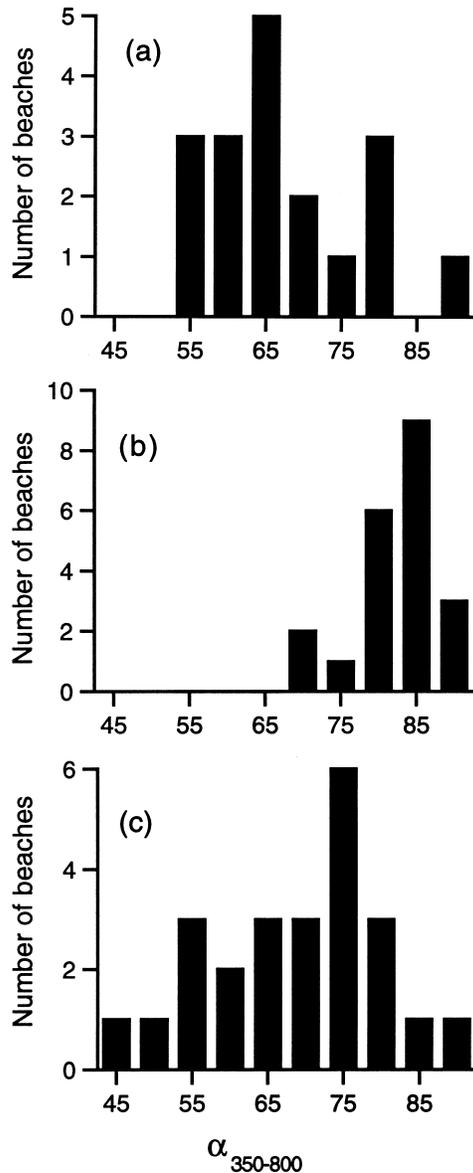

Fig. 3. The range of sand absorptance values measured for beaches (a) at Ascension Island, (b) at Cyprus ($\alpha_{350-800\text{field}}$ values from Fig. 2) and (c) around the world ($\alpha_{350-800\text{lab}}$ values -2.3% to take account of the measured differences between the field and laboratory measurements).

measuring over different ranges of the electromagnetic spectrum. The important point is that the measurements taken using the different techniques need to be highly correlated, i.e. the differences in absorptance that we measure in the field with a lightmeter should accurately represent the true differences. In this context, our field technique is clearly sound. It was interesting that the measured percentage of incident solar radiation absorbed by the different beaches increased slightly between the respective measurements in the field and the laboratory (i.e. $\alpha_{350-800\text{field}}$ and $\alpha_{350-800\text{lab}}$, respectively). This small difference may be because measurements in the field are made on the surface layer and then, when sand is brought into the laboratory, inevitably some is collected from just below the surface and this may have slightly different reflective properties. Regardless, the change in readings between the field and the laboratory was small in absolute terms (mean 2.3%) compared to the range of values from different beaches and hence is unlikely to be important when assessing inter-beach differences.

The finding that sand temperatures increased as the percentage of incident solar radiation absorbed by the sand increased is not unexpected, given that we have previously established this link at Ascension Island (Hays et al. 1995a) (note that in this previous study we used an incorrect value for the albedo from the grey card and hence, while the relative difference in sand albedo between beaches was correctly reported, the absolute values for albedo were overestimated). On Ascension Island, thermal overlap between dark and light beaches rarely occurs either within or between seasons (Hays et al. 1999), with this dichotomy existing because of the limited seasonal change in sand temperature which is presumably related to the equatorial location of the island. Furthermore, individual beaches appear uniform in colour which is presumably the reason why there is very limited within-beach thermal variation at nest depths (Hays et al. 1995a).

In theory, even though the thermal properties of different beaches may vary, their respective incubation temperatures could still be similar if females adjusted their nest position depending on the sand albedo. Such adjustment could occur horizontally (e.g. nesting at different distances from the sea) or vertically (nesting at different depths). However, certainly at Ascension Island, we have strong empirical evidence that neither of these scenarios occur. First, at Ascension, females tend to start digging their nests as soon as they reach the dry sand above the spring high water line, where the beach topography is uneven, i.e. nest site selection appears to be governed by simple rules (Hays et al. 1995b). Second the depth of nests is not adjusted with respect to the albedo of each particular beach (this study). Consequently, the differences in temperatures we have recorded at the same depths on different beaches (e.g. Fig. 2) are mirrored by the between-beach variations in

incubation temperature (Hays et al. 1995a). In short, the albedo of the sand drives large between-beach variations in incubation temperature at Ascension Island.

This importance of sand albedo is clearly not limited to Ascension Island, since the same pattern was evident on Cyprus, i.e. there was a large variation in the sand albedo between beaches driving large thermal variations at nest depth. What was particularly interesting in the Cyprus data was both (1) the magnitude of the sand albedo related thermal differences between beaches, which paralleled the patterns found at Ascension Island and (2) the fact that on Cyprus, which approaches the northern limit for nesting green turtles, the inter-beach thermal differences were again maintained throughout the nesting season with the coolest temperatures recorded on the darker beaches almost always exceeding the warmest temperatures recorded on lighter coloured beaches. This consistency in results from such widely separated rookeries points to a general importance of sand albedo for this species. Both Ascension Island and Cyprus are characterised by a lack of supra-littoral vegetation. It is presumably in these situations where the impact of sand albedo on sand temperature is going to be most marked because there are no shade-induced variations in temperature within individual beaches.

The importance of sand albedo in influencing thermal conditions is reinforced when the temperature during the middle third of incubation is calculated. Cool, male-producing temperatures were found on lighter coloured beaches, while warmer, female-producing temperatures were found on darker beaches. This suggests that the existence of nesting beaches spanning a range of albedos at both rookeries will have major implications for the sex ratios being produced. For example, if only darker beaches occurred on Cyprus, then almost no males would be produced. While this general conclusion regarding the impact of sand albedo on hatchling sex ratio is robust, exactly "how many more males" will be produced on lighter beaches will be dependent on the exact pivotal temperature for turtles at Cyprus and Ascension.

The range of sand albedo values we recorded both at Ascension Island and at Cyprus would appear not to be unusual since a similar range of values was found in the samples collected around the world. This suggests that on a global scale the local thermal conditions within individual rookeries may be strongly dependent on the particular albedo at that site. However, with our very restricted sampling from these beaches around the world we cannot, as yet, infer anything about the variation in sand albedo at these different rookeries. However, certainly in eastern Australia, there is evidence that, like at Ascension Island and Cyprus, between-beach thermal differences are driven by sand albedo (Limpus et al. 1983).

The range of sand albedos available to nesting females within individual rookeries, may also have important implications in scenarios of global climate change. For example, where the albedo of sand from beaches in close proximity is markedly different, large inter-beach thermal variations would be expected which may help to buffer the ecological implications of long-term changes in temperature. In contrast, for nesting areas where the sand albedo is more uniform, then inter-beach thermal variations would be expected to be reduced. In addition, sand albedo may have more immediate conservation implications. For example, where eggs are relocated to hatcheries, the sand albedo within the hatchery will influence the resulting sex ratio of hatchlings; while artificial changes in the sand albedo which might occur, for example, where beaches are nourished with sand dredged from offshore (e.g. Davis et al. 1999), may also change incubation temperatures. In conclusion, we would urge that sand albedo is considered in other studies where incubation temperatures and hatchling sex ratios are examined and we have outlined a cheap, simple and reliable technique for its measurement.

References

Ackerman, R. A. 1997. The nest environment and embryonic development of sea turtles. – In: Lutz, P. L. and Musick, J. A. (eds), The biology of sea turtles. CRC Press, pp. 83–106.

Ciofi, C. and Swingland, I. R. 1997. Environmental sex determination in reptiles. – Appl. Anim. Behav. Sci. 51: 251–265.

Davenport, J. 1997. Temperature and the life-history strategies of sea turtles. – J. Therm. Biol. 22: 479–488.

Davis, R. A., Fitzgerald, M. V. and Terry, J. 1999. Turtle nesting on adjacent nourished beaches with different construction styles: Pinellas County, Florida. – J. Coastal Manage. 15: 111–120.

Godfrey, M. H., D'Amato, A. F., Marcovaldi, M. A. and Mrosovsky, N. 1999. Pivotal temperature and predicted sex ratios for hatchling hawksbill turtles from Brazil. – Can. J. Zool. 77: 1465–1473.

Hays, G. C., Adams, C. and Speakman, J. R. 1993. Reproductive investment by green turtles nesting on Ascension Island. – Can. J. Zool. 71: 1098–1103.

Hays, G. C., Adams, C. R., Mortimer, J. A. and Speakman, J. R. 1995a. Inter- and intra-beach thermal variation for green turtle nests on Ascension Island, South Atlantic. – J. Mar. Biol. Ass. UK 75: 405–411.

Hays, G. C., Mackay, A., Adams, C. R. et al. 1995b. Nest site selection by sea turtles. – J. Mar. Biol. Ass. UK 75: 667–674.

Hays, G. C., Godley, B. J. and Broderick, A. C. 1999. Long-term thermal conditions on the nesting beaches of green turtles on Ascension Island. – Mar. Ecol. Prog. Ser. 185: 297–299.

Janzen, F. J. and Paukstis, G. L. 1991. Environmental sex determination in reptiles: ecology, evolution and experimental design. – Q. Rev. Biol. 66: 149–179.

Limpus, C. J., Reed, P. and Miller, J. D. 1983. Islands and turtles. The influence of choice of nesting beach on sex ratio. – In: Baker, J. T. (ed.), Proceedings of the inaugural Great Barrier Reef conference. James Cook Univ. Press of North Queensland, pp. 397–402.

Milton, E. J., Rollin, E. M. and Emery, D. R. 1995. Advances in field spectroscopy. – In: Danson, F. M. and Plummer, S. E. (eds), Advances in environmental remote sensing. John Wiley and Sons, pp. 9–32.

Milton, E. J., Emery, D. R. and Kerr, C. H. 1997. NERC Equipment for field spectroscopy: preparing for the 21st century. – In: Griffiths, G. and Pearson, D. (eds), Observations and interactions. Proceedings of the 23rd Annual Conference of the Remote Sensing Society, Remote Sensing Society, Nottingham, UK, pp. 159–164.

Morreale, S. J., Ruiz, G. J., Spotila, J. R. and Standora, E. A. 1982. Temperature-dependent sex determination – current practices threaten conservation of sea turtles. – Science 216: 1245–1247.

Mrosovsky, N., Hopkins-Murphy, S. R. and Richardson, J. I. 1984. Sex-ratio of sea turtles – seasonal changes. – Science 225: 739–741.

Pieau, C. 1972. Effets de la température sur le développement des glandes génitales chez les embryons de deux Chéloniens, *Emys orbicularis* L. et *Testudo graeca* L. – C.R. Acad. Sci. Paris 274: 719–722.

Rhen, T. and Lang, J. W. 1998. Among-family variation for environmental sex determination in reptiles. – Evolution 52: 1514–1520.

Shine, R. 1999. Why is sex determined by nest temperature in many reptiles? – Trends Ecol. Evol. 14: 186–189.

Vermote, E. F., Tanre, D., Deuze, J. L. et al. 1997. Second simulation of the satellite signal in the solar spectrum, 6S: an overview. – IEEE Trans. Geosci. Remote Sens. 35: 675–686.