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Measuring the state of consciousness in a free-living diving sea turtle

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Abstract

We report on results from two types of data-logger attached to hawksbill turtles (*Eretmochelys coriacea*) in the breeding season at the Seychelles, Indian Ocean. Conventional time–depth recorders (TDRs) showed prolonged bouts of long dives to the seabed, consistent with benthic resting. This behaviour has been widely reported in sea turtles and appears to be a common feature for energy conservation. An Inter-Mandibular Angle Sensor (IMASEN) recorded mouth opening and buccal pumping by one turtle for 2.5 days. Buccal pumping occurred widely while the turtle was submerged, consistent with a function of olfactory sensory perception of the turtle's environment. However, buccal pumping stopped during the middle of long benthic dives consistent with the turtle entering a phase of sleep. It therefore appears that by recording buccal oscillations, it is possible to assess the state of consciousness of turtles allowing the eco-physiology of diving to be more fully explored.
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Keywords: Bird; Dive function; Gular; Mammal; Rest; Sleep

1. Introduction

Over recent years our understanding of the free-living behaviour of marine vertebrates has been transformed through the use of data-loggers and transmitters that can provide information on various aspects of the behaviour of individuals and their environment (e.g. Sims et al., 2005; Metcalfe et al., 2006). Dive profiles are now routinely measured with time–depth recorders (TDRs) (e.g. Rice and Balazs, 2008-this issue; Ropert-Coudert and Wilson, 2005) some linked to satellite transmitters (Myers et al., 2006). However, depth data is increasingly supplemented by other measurements such as swimming effort (e.g. measured with accelerometers or swim speed recorders); patterns of feeding (e.g. measured with stomach temperature recorders, visual imaging recorders or mouth-opening sensors) (Ropert-Coudert and Wilson, 2005). Information is therefore starting to be gleaned on how animals partition their time between various activities such as travelling, feeding and breeding (Beck et al., 2003; Fowler et al., 2006). Much recent attention has focussed on patterns of foraging given the central component of feeding in the life history of vertebrates (e.g. Austin et al., 2006; Myers et al., 2006; Watwood et al., 2006). However, some behaviours which may similarly be very important, have received much less attention.

Resting forms a vital component in the time-budget of all vertebrates. For some marine vertebrates, resting may take place on land, such as seals that haulout to rest ashore, making the time spent resting fairly easy to measure by direct observation. However, for other marine vertebrates that do not haul ashore to rest, we can infer that resting presumably takes place at sea, potentially on the sea surface, in mid-water or on the seabed. For example, some whales are thought to sleep at the surface when their behaviour is described as "logging" (Goold, 1999; Lyamin et al., 2000). It has been suggested that some species of seal may rest in mid-water, during which time they may passively drift down or up in the water column depending on their state of buoyancy (Biuw et al., 2003; Page et al., 2005). It

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is thought that dolphins may be able to sleep while continuing to swim, sometimes keeping one eye open beneath the surface (Lyamin et al., 2004; Sekiguchi et al., 2006). However, it is sometimes difficult to unequivocally resolve the function of dives even when diving animals are directly observed in aquaria (e.g. Lyamin et al., 2006). In such cases direct measurements of an animal's state, for example from electroencephalogram readings, may be needed (Lyamin et al., 2004).

Hard-shelled turtles, both marine and freshwater species, appear to be unusual amongst air-breathing divers in that they typically rest on the bottom, often for extended periods, during demersal stages of their life cycle. For example, dives to the seabed of >30 min have regularly been recorded for green (*Chelonia mydas*) (Hays et al., 2004a), hawksbill (*Eretmochelys imbricata*) (van Dam and Diez, 1996; Storch et al., 2006) and loggerhead (*Caretta caretta*) turtles (Houghton et al., 2002). In winter, when water temperatures are low, dives of over 6 h have been recorded for marine species, while freshwater turtles may sometimes stay submerged for many weeks during winter (see Hochscheid et al., 2005a and references therein). For free-living individuals, resting behaviour has generally been inferred from examination of dive profiles rather than being directly recorded. However, hard-shelled sea turtles show characteristic behaviours when resting, which might be directly recorded allowing their behavioural state to be unequivocally identified. Walker (1959) first noted that while submerged hard-shelled turtles are awake, they have their eyes open (in common with many other vertebrates) and also show continuous rhythmic throat movements termed buccal oscillations (sometimes called gular pumping). Buccal oscillations generate a steady flow of water pass the chemosensory organs and, in essence, the behaviour corresponds with turtles smelling the water, presumably for detection of prey, predators, or other individuals (Manton et al., 1972a,b). Walker (1959) noted that when turtles closed their eyes for extended periods (presumably sleeping) buccal oscillations ceased. In essence, therefore, buccal oscillations seem to give an indication of the state of consciousness for submerged hard-shelled turtles. Recently, Hochscheid et al. (2005b) used a device termed the IMASEN (Inter-Mandibular Angle Sensor) to measure buccal oscillations in captive loggerhead turtles. Buccal oscillations were associated with very small openings of the mouth (Hochscheid et al., 2005b). In line with the visual observations of Walker (1959), Hochscheid et al. (2005b) used an IMASEN to record the cessation of buccal oscillations when loggerhead turtles rested on the bottom of tanks with their eyes closed. Hochscheid et al. (2005b) suggested that IMASENs deployed on free-living animals might be used to record the state of consciousness of turtles while on the seabed. To explore this possibility, we deployed an IMASEN on a free-living hawksbill turtle in the internesting interval and recorded the extent of gular pumping along with dive profiles.

Table 1
Details of successfully instrumented hawksbill turtles

Turtle id	Equipment deployed	Deployment date	Length of dive record	CCL (cm)
2929	TDR	28/10/2004	16 days	80
3089	TDR	30/10/2004	14 days	80
2969	TDR+IMASEN	31/10/2004	15 days	80
2872	TDR	2/11/2004	28 days	90

TDR = time–depth recorder. CCL = curve carapace length (cm).

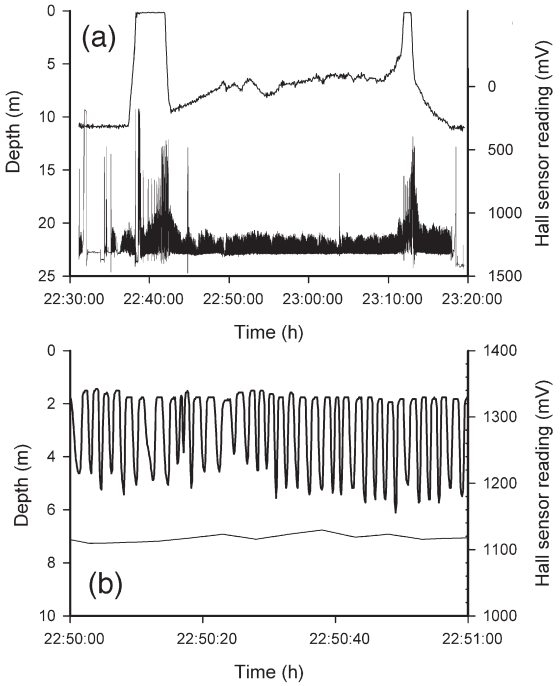

Fig. 1. Typical IMASEN and depth traces from an active dive. Thin line = depth, thick line = Hall sensor readings. Part (a) shows the complete dive, part (b) shows 1 min during the dive. Note variation in depth indicative of turtle activity, with the turtle ascending from about 10 m up to 6 m during the dive. The values recorded by the IMASEN (mV) give a relative measure of mouth gape. When the mouth was closed the Hall sensor and magnet would be closer together giving higher reading (~1300 mV). When the mouth opened, the Hall sensor and magnet would become further apart producing lower values. When at the surface, wide mouth-opening events were recorded. When submerged the trace shows regular small amplitude mouth-opening events.

2. Materials and methods

We attached an IMASEN (Driesen and Kern, Bad Bramsted, Germany) to a hawksbill turtle that had completed nesting on Curieuse Island Marine National Park in the granitic Seychelles (4°16.827′ S; 55°44.462′ E). Close (within 5 km) to the island are water depths up to 30 m. The IMASEN (5.5×3.4 cm, 27.6 g in air) consists of a Hall sensor, linked to a data-logger, which measures the proximity of a nearby magnet. By positioning the Hall sensor on the upper mandible of the turtle and a neodymium boron magnet on the lower mandible, we recorded when the turtle opened its mouth (see Myers and Hays (2006) for a schematic of attachment). While the raw values (mV) recorded by the IMASEN gave a relative measure of mouth opening, we were unable to convert these values into absolute gape distances (mm) because the turtle re-entered the water before we could complete validation measurements. The IMASEN sampled at 10 Hz and at this sampling frequency the logger memory was filled in 2.5 days.

Table 2
The number of U-dives and their depth and duration recorded for hawksbill turtles in the Seychelles

Turtle id	U-dives		
	Mean depth (m) (*n*, SD, maximum)	Mean duration (min) (*n*, SD, maximum)	Percentage of time
2929	4.5 (567, 2.2, 26.6)	28.2 (567, 8.7, 63.2)	69.2
3089	9.1 (403, 3.5, 30.0)	31.3 (403, 8.3, 55.0)	61.9
2969	11.6 (336, 1.8, 30.6)	49.2 (336, 9.6, 67.8)	77.5
2872	19.9 (479, 1.1, 55.3)	45.7 (479, 14.9, 79.5)	52.9

The Hall sensor and magnet were attached to the upper and lower jaws respectively with quick setting epoxy (Loctite "Super Glue") (see Myers and Hays, 2006) with the output lead running to a data-logger attached to the head with a second type of quick-set epoxy that also provided protection to the logger (David's Isopon P40). In addition a time–depth recorder (LTD 1200, LOTEK Marine Technologies, St. John's, Newfoundland) was attached to the carapace and recorded depth every 5 s. For a further three turtles we obtained dive records by attaching only a TDR to the carapace (Table 1). Equipment was removed when turtles returned to nest later that season. In three cases this corresponded with the subsequent nesting event (internesting intervals 16, 14, 15 days respectively). In one case (turtle id 2872) the logger was retrieved after about one month. In this case the TDR memory has filled up after 28 days. This turtle had nested unobserved after 15 days, as evidenced from the dive trace.

We used bespoke data analysis software (MultiTrace for Windows, Jensen Software Systems, Laboe, Germany) to analyse the dive and IMASEN data. This software allowed data visualisation and automated extraction of several parameters from each dive, including maximum depth and dive duration. We defined dives as those when a depth of ≥ 1 m was attained. U-dives were identified by eye as those when there was minimal variation during the bottom phase of dives (see Fig. 1). Dive data were corrected for sensor drift (only a few cm during deployment) by "zero point calibration". To do this we examined the TDR data for the shallowest depth recorded every 6 h, on the assumption that this would be the surface (0 cm). We quantified the frequency of mouth opening during dives using the 'Count Events' function of Multitrace, which measures how often the Hall sensor reading crosses a threshold value over a selected period. This threshold value was selected in line with the amplitude of the signals received during buccal oscillations.

3. Results

All the turtles showed prolonged periods of U-dives to the sea floor, during which there was very little variation in the bottom phase. The typical depth of U-dives varied between 4 and 20 m depending on the individual turtle and typical durations were 30–50 min (Table 2).

The IMASEN data revealed how a turtle opened its mouth for the 2.5 days after nesting. During the first day after entering

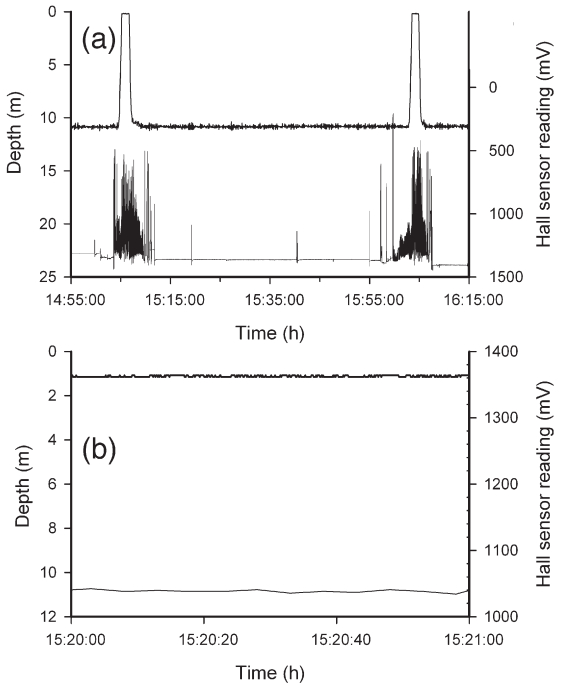

Fig. 2. Typical IMASEN and depth traces from a long U-dive to about 11 m. Thin line = depth, thick line = Hall sensor readings. Part (a) shows the complete dive, part (b) shows 1 min during the dive. Note that in contrast to Fig. 1 there is little variation in depth during the bottom phase, with the turtle remaining at 11 m. The values recorded by the IMASEN (mV) give a relative measure of mouth gape. When submerged the trace shows very little mouth opening.

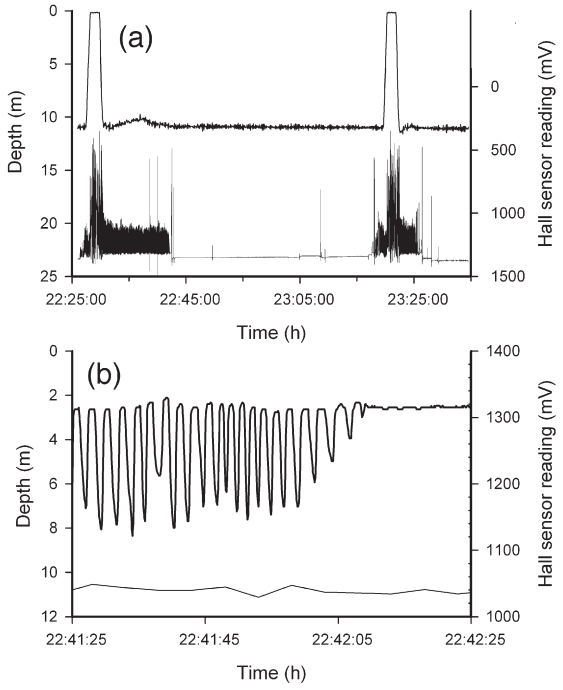

Fig. 3. IMASEN and depth traces from a long U-dive to around 11 m, where there was initially some variation in depth indicative of activity. About 10 min into the dive the variation in depth ceased and there was an abrupt cessation of rhythmic mouth openings. Part (a) shows the complete dive, part (b) shows 1 min during the dive and highlights when rhythmic mouth openings ceased at about 22:42:10. The values recorded by the IMASEN (mV) give a relative measure of mouth gape.

Fig. 4. The mean rate of mouth opening during a dive, i.e. excluding time at the surface, compared to dive duration. The longest dives were always associated with little mouth opening.

the water there was a pattern of near-continuous mouth opening associated with short dives (Fig. 1a). When the turtle was at the surface there were higher amplitude mouth-opening events (Fig. 1a). Detailed examination of these periods of mouth opening when the turtle was submerged showed that they consisted of rhythmic opening and closing (Fig. 1b). The turtle soon started to conduct longer U-dives during which there were often long periods when the mouth remained closed, with the general exception of the start and end of the bottom phase of these dives (Fig. 2). Sometimes during dives there was a clearly demarked time when mouth opening ceased (Fig. 3).

The frequency of mouth opening while the turtle was submerged was less on longer dives (Fig. 4). For example, for dives of >40 min duration, the mean rate of mouth opening while submerged was always <0.1 Hz, but this mean rate increased to >0.5 Hz for some dives of <10 min.

There was some individual variation in the temporal patterns of dive duration over the internesting interval. However a consistent pattern for different individuals was that the shortest dives were always recorded in the 3 days preceding the subsequent nesting event (Fig. 5). For example, for turtle 2969 the mean daily dive duration increased to around 50 min by day 12 of the internesting interval, but then decreased to around 10 min in the 3 days preceding the next nesting event.

4. Discussion

The mouth-opening events we recorded here for a free-living hawksbill turtle are entirely consistent with the buccal oscillations recorded in submerged loggerhead turtles in captivity by Hochscheid et al. (2005b). These buccal oscillations are characterised by a lower amplitude than breathing at the surface and are very regular, unlike mouth opening associated with prey capture and ingestion. The frequency and relative amplitude of mouth-opening events that we recorded were readily apparent, and our results show that measurements of buccal oscillations are now possible in the wild. It was clear that during long U-dives there was little mouth opening. These observations support the contention (van Dam and Diez, 1996; Hays et al., 2004a) that long U-dives have a resting function for sea turtles. Clearly we also measured other mouth-opening movements (e.g. associated with breathing at the surface). In other words a single IMASEN can potentially measure several aspects of behaviour including buccal oscillations, breathing and feeding.

There are several methods of recording the activity of diving animals. Simple TDRs record the extent of vertical movement, while flipper beating can be recorded in several ways to indicate the extent of active swimming (e.g. Hays et al., 2004b; Hays et al., 2007; Wilson and Liebsch, 2003). However, sometimes

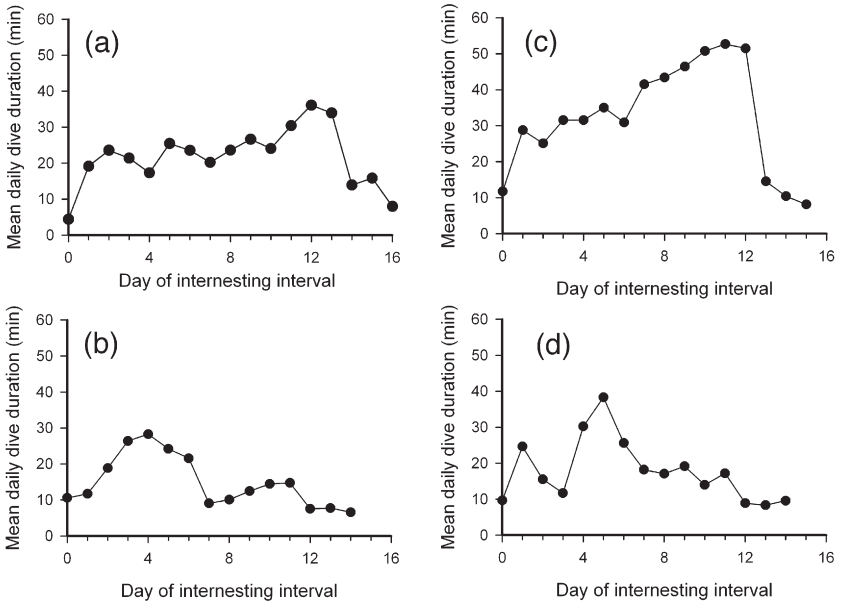

Fig. 5. For four equipped hawksbill turtles the proportion of time spent conducting U-dives during the internesting interval. (a–d) Turtles 2929, 3089, 2969 and 2872 respectively. Each internesting interval shown was recorded in its entirety.

an animal may be at a single depth, but still be active (e.g. during benthic foraging). In such cases activity may be revealed by a compass (e.g. Storch et al., 2006) or animal-borne cameras (e.g. Seminoff et al., 2006). However recording whether a diver is awake or asleep is more problematic as inactive animals may be in either state. The standard method of recording periods of sleep in vertebrates is from electroencephalogram readings (Lyamin et al., 2004). This involves placing external electrodes on the head. Such measurements have generally been confined to captive animals. The use of IMASEN recorders provides an alternative method for objectively assessing periods of sleep in turtles, extending the use of these devices beyond that previously described for free-living turtles (Myers and Hays, 2006, 2007). These devices therefore extend the behavioural data which can be derived from free-living turtles.

Our IMASEN results for hawksbill turtles are in contrast to those we have recently reported for leatherback turtles (Myers and Hays, 2006). In the internesting period in the Caribbean, leatherback turtles range widely, moving up to several hundred km during a single internesting interval, and dive deeply, sometimes to several hundred metres (Georges et al., 2006; Myers and Hays, 2006). The diel pattern of their diving is consistent with leatherbacks tracking their prey located in planktonic deep-scattering layers, with these layers being found closer to the surface at night. IMASEN data suggest that leatherback turtles show buccal oscillations on the dive descent consistent with olfactory detection of prey (Myers and Hays, 2006). Hence while IMASEN data have revealed how leatherback turtles search for prey during the internesting period, they reveal how hawksbill turtles enter a resting state on the seabed soon after nesting.

Interestingly, even when there was no regular mouth opening during the bottom phase of dives, the IMASEN data revealed that regular mouth opening often resumed prior to the turtle ascending to the surface. The implication is that sleeping turtles wake up some time before they ascend at the end of the dive. Presumably this behaviour is associated with the turtle re-establishing a state of awareness for its environment before it moves, giving it the time to detect potential predators or other hazards. This idea is consistent with evidence that predators play important roles in shaping the behaviour of turtles through all their life-history stages (Heithaus et al., 2007, 2008-this issue). Certainly for a range of diving animals it has been suggested that the surface may be a risky place because the diver is silhouetted and so more visible to predators and also has fewer options for escape since its potential escape directions are partly constrained by the surface (Heithaus and Frid, 2003). Hence it makes sense for a surfacing turtle to make some initial preparations before it ascends following a period of sleep.

For hard-shelled marine turtles it appears that at many rookeries, resting dives form an important component of the internesting behaviour of female turtles. While this is not universally true (see for example Hays et al., 2002), the implication is that female hard-shelled turtles often have a strategy of energy conservation during the internesting period which presumably allows them to maximise their reproductive output. However, we recorded distinct patterns for the duration of dives during the internesting period. Generally, a few days before the subsequent nesting event, the mean dive duration decreased. The implication is that turtles were more active in the days prior to nesting. This pattern of increasing activity as a nesting event approaches, has been inferred several times before for sea turtles. Hays et al. (1991) used the pattern of uplinks from a satellite tag to infer that an internesting loggerhead turtle in the Mediterranean spent longer at the surface as nesting events approached. Similarly using limited data on dive duration relayed from satellite tags attached to green turtles at Ascension Island, Hays et al. (1999) showed a decrease in dive duration as nesting events approached, consistent with a reduction in the occurrence of U-dives. Our results for internesting hawksbill turtles extend these previous observations with loggerhead and green turtles and suggest that increasing activity towards the end of internesting intervals may occur widely in hard-shelled marine turtles. Clearly it would be interesting to record the pattern of buccal oscillations throughout entire internesting intervals to more critically examine these inferences of patterns of activity. The reasons for this pattern of activity are uncertain. However one possibility is that nesting beach selection may be a protracted affair. Certainly the choice of nesting beach may be a vital factor in driving the survival of eggs (Lee and Hays, 2004), with some beaches having suboptimal conditions. Hence it might be expected that turtles would spend some time selecting a suitable location and time for nesting. Furthermore there is striking evidence both from flipper tagging turtles and molecular studies that female turtles show degree of fidelity to particular nesting beaches, which supports the suggestion of active selection of the nesting beach. However, the processes involved in beach selection remain unknown.

In conclusion our results extend the utility of recording mouth opening in marine vertebrates. Such measurements can inform on breathing rates at the surface, feeding events while submerged and efforts to detect prey (Wilson et al., 2002; Myers and Hays, 2006) and also the state of consciousness of an animal (this study). Following work with internesting turtles (this study and also Myers and Hays 2006) one key focus for further work should be to make measurements of mouth opening for turtles on their foraging grounds.

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