



The diving behaviour of green turtles at Ascension Island

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For six green turtles, *Chelonia mydas*, that had nested on Ascension Island in the South Atlantic, we used time–depth recorders to examine their diving behaviour during the subsequent interesting interval (10–12 days). All the turtles performed dives where they remained at a fixed depth for a long period, surfaced briefly and then dived to the same depth again. It is generally believed these dive profiles are caused by the turtles resting on the sea bed. The maximum depth that turtles routinely reached on these resting dives was between 18 and 20 m, with resting dives deeper than 20 m being extremely rare. Resting dive duration increased significantly with deeper dives. From this relationship, and assuming that turtles with fully inflated lungs at the surface need to dive to 19 m to achieve negative buoyancy, we estimated for two turtles that the oxygen consumption during resting dives was 0.016 and 0.020 litres O₂/kg per h, respectively. This is similar to the value predicted from the allometric scaling relationship for the minimal oxygen consumption of turtles. We calculated that the energy conserved by resting during the interesting period may appreciably increase the reproductive output of females.

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A fundamental component of many ecological studies is how animals allocate time to different behaviours. This area of science is particularly well developed for terrestrial species since they can often be readily observed. In contrast, marine animals present a more intractable problem since they may remain submerged, and hence out of view, for long periods. This dichotomy between terrestrial and marine studies is reflected in our knowledge of sea turtles in their natural habitats. On the one hand, observations on nesting beaches have been relatively straightforward to make, leading to many studies that have examined aspects such as body size, clutch and egg size, nesting behaviour, hatchling success and individual nesting periodicity. On the other hand, studies of sea turtles while they are at sea have traditionally been more difficult to make and so have been limited to sporadic observations of their behaviour and fragmentary evidence of long-distance movements from mark–recapture studies (for example see Dodd 1988 for a review).

This imbalance in information is, however, starting to be redressed with the advent of small, reliable data-logging and tracking devices. For example, satellite tracking has identified the routes that turtles follow during their migrations between nesting and feeding areas (e.g. Luschi et al. 1998) while implanted temperature loggers have been used to examine aspects of their thermoregulatory capacity (Sato et al. 1994). Similarly, the advent of reliable time–depth recorders has begun to allow the diving behaviour of free-ranging turtles to be documented (Eckert et al. 1989). These recorders have, for example, been used to distinguish periods of inactivity, where turtles remain resting on the sea floor for long periods, from bouts of activity where the depth of the animal varies constantly (van Dam & Diez 1996). It has been shown experimentally that, for the loggerhead turtle, *Caretta caretta*, individuals control their buoyancy by varying the volume of air inspired immediately prior to submergence (Milsom 1975). Consequently, Milsom (1975) suggested that when the turtle embarks on a deep dive, a greater volume of air is inspired so that neutral buoyancy is attained at a greater depth. As a corollary to this hypothesis, it would be predicted that if more air is inspired before deeper dives, then the available oxygen stores will be greater and hence dive duration will increase. Data from time–depth recorders have, indeed, shown that for loggerhead turtles dive duration increases

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Table 1. Details for the six turtles from which time–depth recorders (TDRs) were recovered, including the mean percentage of time spent resting by each individual

Turtle number	Curve carapace length (cm)	Manufacturer of TDR (model and weight in air)	Data logging interval (s)	Depth resolution	Time spent resting (%)
1	109.0	Wildlife Computers (Mk 6, 125 g)*	10	2 m	49.9
2	127.75	Wildlife Computers (Mk 6, 125 g)	10	2 m	36.2
3	124.0	Vemco (Minilog TX, 23 g)†	150	30 cm	37.8
4	115.0	CEFAS (Mk 1, 55 g)‡	300	10 cm	20.9
5	124.5	CEFAS (Mk 1, 55 g)‡	300	10 cm	67.5
6	114.5	CEFAS (Mk 1, 55 g)‡	300	10 cm	31.7

*Wildlife Computers, Redmond, U.S.A.

†Vemco, Shad Bay, Nova Scotia, Canada.

‡The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft, U.K.

with dive depth, supporting the idea of active control of buoyancy through lung volume with a consequent limit to dive duration (Minamikawa et al. 1997).

Despite these recent advances, huge gaps remain in our understanding of the physiology and ecology of turtles while they are at sea. A major challenge is to understand the energetics of reproduction in these species, many of which undertake very extensive migrations between feeding and nesting areas. For some populations, such as the green turtles, *Chelonia mydas*, that feed on the South American coast and nest on Ascension Island, there is little food available both during migration and at the nesting area. Therefore, the cost of reproduction in these populations includes the energy investment in migrating (the minimum round trip from South America to Ascension Island is 4400 km), the cost of remaining at the nesting area for several weeks while consecutive clutches are laid, the cost of emerging on to beaches to excavate nests, deposit the eggs and then cover the site, and the structural investment in the eggs themselves. However, while there are some figures for the metabolic rate of adult turtles while they are on beaches (e.g. Jackson & Prange 1979), there are no measurements of the metabolic rates of free-ranging animals at sea.

We used time–depth recorders to quantify the interesting diving behaviour of green turtles at Ascension Island. From the diving data we set out to infer periods when the turtles were resting on the sea bed and then, by examining the relationship between dive duration and dive depth, we constructed a bioenergetic model to estimate the resting metabolic rate of the turtles and hence their aerobic dive limits. We also considered the implications for the fat reserves needed to sustain turtles during the interesting period.

METHODS

Dive Data

Between 20 and 23 March 1998, we attached time–depth recorders (TDRs) to eight green turtles that were nesting on Long Beach, Ascension Island (7°57'S, 14°22'W). Three different types of TDR were used, each

with different sampling characteristics (Table 1). The recorders were attached with either cable ties, stainless steel wire or screws (depending on the model of TDR) to base plates glued on to the heads of the turtles with a quick-setting epoxy (David's Isopon P.40) which we have previously used successfully to secure devices to turtles (Hays et al. 1991). Attachment was completed in about 25 min. The curve carapace length (CCL) was measured with a flexible tape.

We then patrolled the beach at night to try to intercept these turtles if they returned to nest. We could remove the TDRs in only a few seconds by either cutting the cable ties or stainless steel wire, or removing the screws that attached the TDR to the base plate. In all, six of the recorders were recovered when the turtles returned to nest with intervals of between 10 and 12 days. Data from the recorders were then downloaded on to a laptop computer.

Turtle Weights

The turtles to which TDRs were attached were not weighed. However, in 1999 we began weighing turtles on a suspended scale (Salter Model 233-10, capacity 300 kg). After nesting, turtles were turned upside down on to cargo netting, hoisted vertically with a hand-operated hoist, and suspended from the scale.

Ethical Note

We used a standard technique, used by our group since 1990, for TDR attachment. When this technique was used on a turtle in an aquarium, no changes in behaviour were noted. For example, the turtle did not try to rub off the unit. Similarly, there was no visible reaction by the turtles either during the attachment procedure or subsequently on the beach. We attached TDRs to the bony plates on the turtle's head and again, from aquarium observations, we know that unless removed by ourselves, everything falls off the turtle after a few months owing to the natural sloughing off of the bony plates. In the past, we have attempted to attach devices to the carapace of green

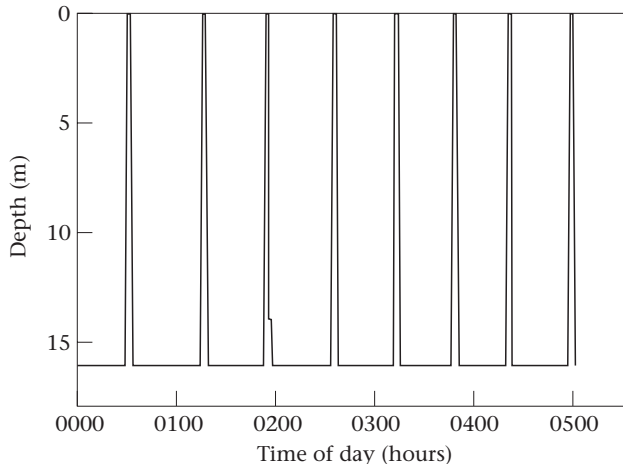


Figure 1. A typical bout of resting dives for turtle 2 between 0000 and 0500 hours.

turtles at Ascension Island. There are problems associated with this approach because the turtles are large (>150 kg) and engage in strenuous mating activity. The result is that devices attached to the carapace are more likely to be destroyed. With small units, the head is therefore the logical place for attachment. In addition, while tortoises can retract their head into the shell, this is not possible for turtles and again this means we see no effect of a small head attachment. Furthermore the TDRs are tiny (≤ 125 g) in comparison with the size of the turtles (>150 kg). The turtles were not restrained either during attachment or removal of the TDRs. We simply observed the turtles from a distance through a night-vision scope and, once they were nesting and so not easily disturbed, attached or removed the units.

The turtles were inverted for about 15 min during the weighing procedure during which time they were quiescent. After weighing there were no visible effects on the turtles' behaviour and they simply crawled back to the sea as usual.

RESULTS

Dive Classification

A range of different dive profiles were observed. However, all the turtles performed dives where they remained at a fixed depth for a long period, surfaced briefly and then dived to the same depth again (Fig. 1). We assumed that such dives, with a flat phase between the initial descent and final ascent, were caused by the turtles resting on the sea bed. Although different TDRs were used, data from only the Wildlife Computers TDRs were fully analysed because of their high temporal resolution. Resting dives were generally very obvious when the dive profiles were plotted. However, to provide consistency we drew up a set of objective criteria for what constituted resting dives. These criteria, although cumbersome, will also allow directly comparable work in future studies.

All dives (both periods of activity and inactivity) were defined as starting when the turtle submerged below 3 m. To eliminate any periods spent just below the surface, a single dive was registered when a turtle (1) was below 3 m for at least 40 s continuously, (2) was below 3 m for at least 50 out of 60 s, or (3) reached a depth of 6 m. A surfacing event was defined as when a turtle either (1) reached a depth of 0 m or (2) was shallower than 3 m for more than 40 out of 50 s. When either of these criteria was satisfied, the dive was recorded as having ended when the turtle reached 3 m on ascent. The period between the end of one dive and the start of the subsequent one was called the surface period.

A resting dive was defined first as a dive having a maximum depth of at least 6 m. Second, the turtle needed to remain within 2 m of the maximum depth for 90% or more of the dive duration (to account for the resolution of the Wildlife Computers recorders). Third, there had to be no systematic linear change in depth during the flat phase of the dive profile and fourth, there had to be at least two consecutive dives fitting these criteria since resting dives typically occurred in distinct bouts. Individual surfacing events could be missed with the lower temporal resolution of the other four loggers (Table 1) and hence, for these four turtles, we used the above criteria to define when turtles were engaged in resting bouts and not when the individual dives started and stopped.

Spatial and Temporal Patterns of Resting Dives

All six turtles spent much of the time during the interesting period engaged in resting dives. However, there was some interindividual variability with, for example, turtle 4 spending relatively little time resting (20.9%) and turtle 5 spending relatively longer resting (67.5%; Table 1). For all six turtles there was a diel pattern to their diving behaviour, with a greater proportion of the time spent resting at night than during the day (Fig. 2).

There was some variation in the modal depth during resting dives for the different turtles (Fig. 3). For example, for turtles 1, 3, 5 and 6 the modal depth was between 16 and 18 m while for turtle 4 it was 6 m. However, all the turtles routinely dived to a maximum of 18–20 m, with dives deeper than 20 m being extremely rare.

For the two turtles for which the length of individual resting dives could be quantified, dive duration was always less than 1 h. For turtle 1 there was a bimodal distribution in the length of dives with peaks around 20 and 42–44 min, while for turtle 2 the frequency distribution of dive duration was unimodal with a peak around 42 min (Fig. 4).

A total of 259 and 165 resting dives were recorded for turtles 1 and 2, respectively, with mean depths and durations \pm SD of 12.1 ± 5.2 m and 28.6 ± 13.2 min and 14.3 ± 3.6 m and 36.0 ± 11.7 min, respectively. For both these turtles, dive duration increased significantly with deeper dives (Fig. 5). For example, using the fitted regression equations (legend to Fig. 5), the mean durations of dives to 6 and 16 m were 15.7 and 36.7 min, respectively,

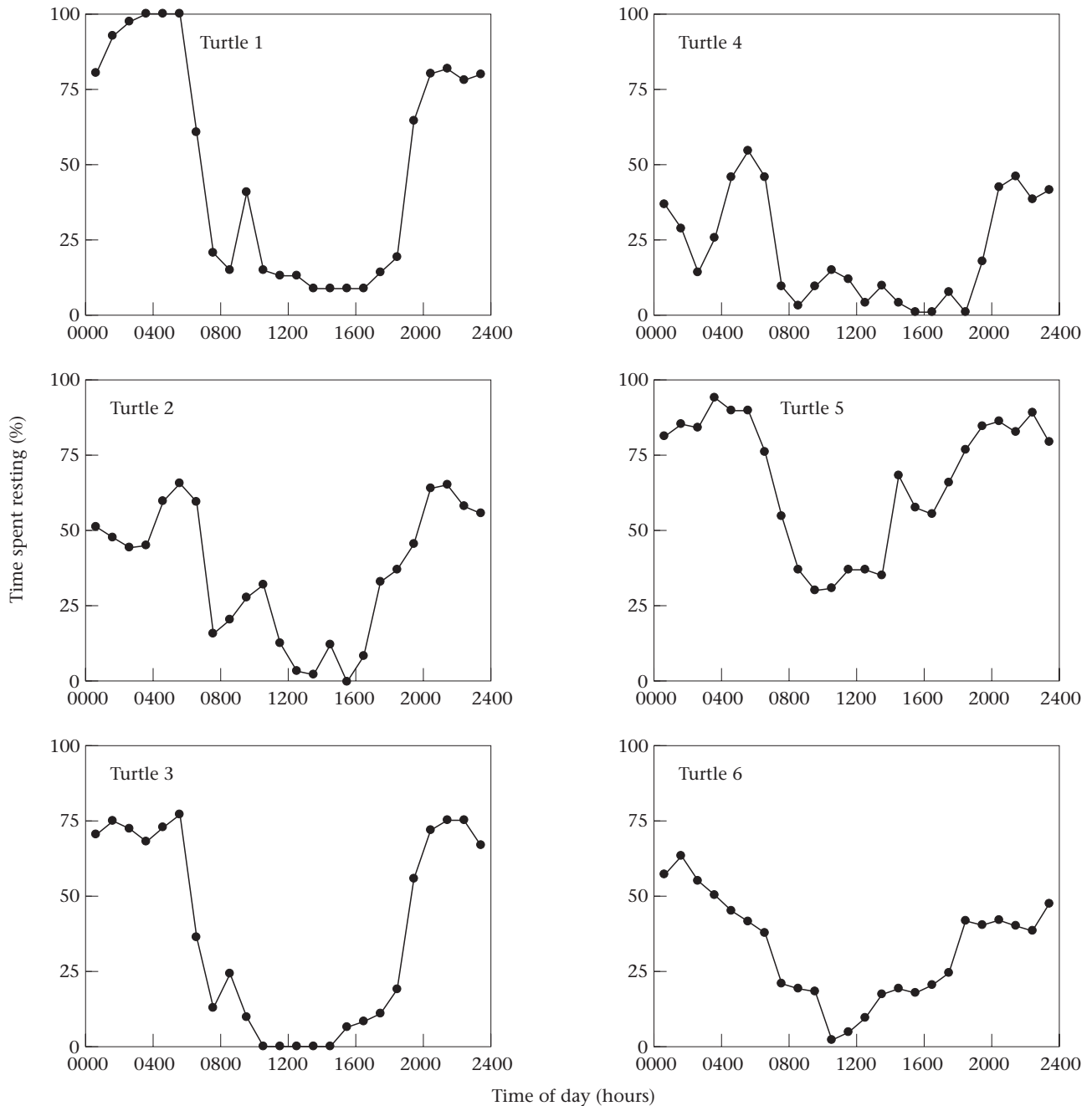


Figure 2. The percentage of time spent resting during the day and night for the six turtles. The times of sunrise and sunset were 0700 and 1900 hours, respectively. The value for each point was calculated by dividing the total time spent resting in that hour of the day during the interesting period by the total duration of depth data for that particular hour of the day.

for turtle 1 and 22.3 and 38.9 min, respectively, for turtle 2.

When assessing postdive surfacing intervals, we ignored the interval after the last dive in a resting bout since it identified the start of the subsequent period of activity. The mean lengths \pm SD of surfacing intervals were 1.7 ± 0.7 min ($N=235$) and 2.2 ± 0.7 min ($N=133$) for turtles 1 and 2, respectively. Postdive surfacing intervals increased significantly after longer resting dives (Fig. 6) but were always less than 4.5 min for both turtles.

Buoyancy Control and Metabolic Rate

We developed the conceptual framework for the model of buoyancy control and metabolic rate during resting dives by building on the following axioms. First, we assumed that the lung volume was used to control buoyancy so that when resting on the sea bed turtles were always neutrally buoyant (in practice a turtle would need to be very slightly negatively buoyant). Second, based on literature values, we assumed that the lung capacity of a green turtle was 9.4% of its weight (Berkson 1966; Lutz &

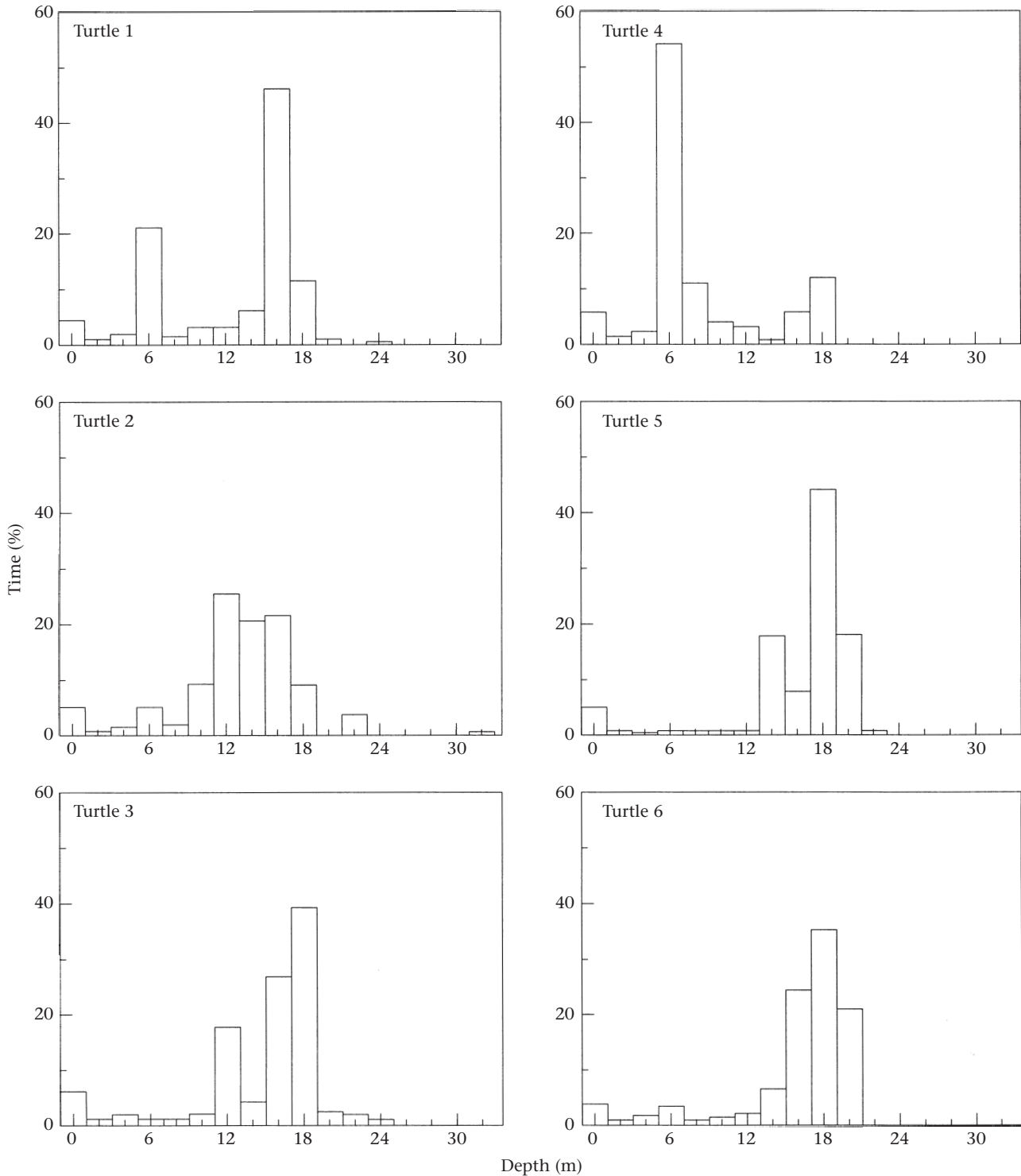


Figure 3. The percentage of time spent at different depths during resting dives for the six turtles. The graphs include time spent on descent and ascent (and hence include shallow depths) as well as time spent at the maximum depth.

Bentley 1985), that the oxygen content of the lungs at the start of a dive was 17.4% (Berkson 1966) and that the blood and muscle of a green turtle can hold 6.7 ml O₂/kg (Lutz & Bentley 1985). Third, we assumed that as a turtle dives the lungs will be compressed in accordance with Boyle's Law. Since the maximum depth that turtles

routinely dived to was 18–20 m (Fig. 3), we assumed that 19 m was the depth at which negative buoyancy was attained if the turtle inhaled fully before diving. Finally, we assumed that regardless of the depth of a dive, turtles always surfaced when their oxygen stores had been decreased to the same level.

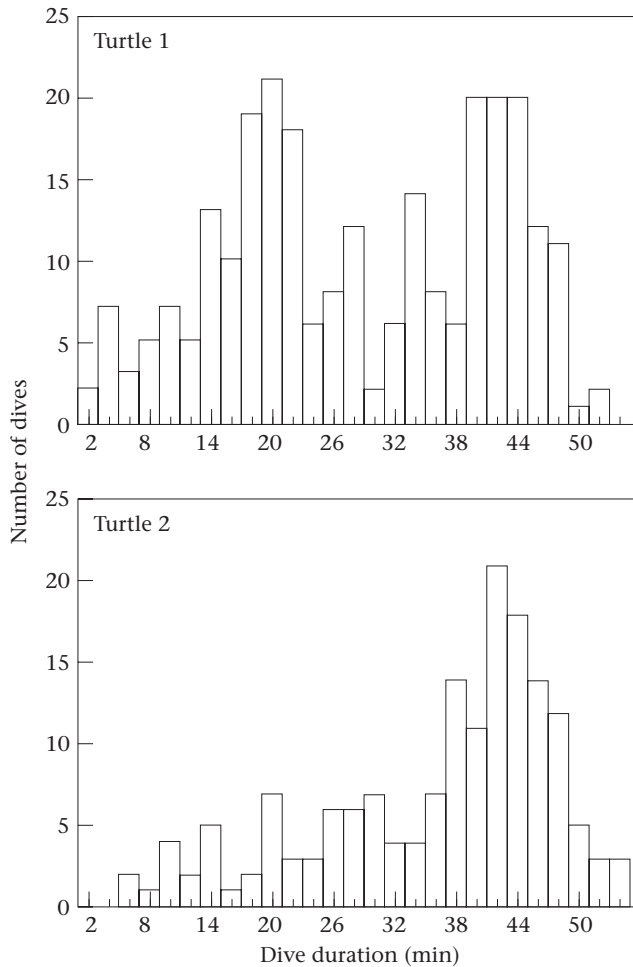


Figure 4. The duration of individual resting dives recorded for turtle 1 and turtle 2.

The weight of Ascension Island green turtles increased significantly with their curve carapace length (CCL; Fig. 7). Using the regression equation relating weight to CCL (legend to Fig. 7) the predicted weight for turtle 1 with a CCL of 109 cm was 150.6 kg and for turtle 2 with a CCL of 127.75 cm it was 236.5 kg.

For turtle 1, the tissue and blood stores will be $150.6 \times 0.0067 = 1.009$ litres of oxygen. The lung capacity will be $150.6 \times 0.094 = 14.156$ litres of air, which equates to 2.463 litres of oxygen at the start of a dive and hence a total oxygen store (lungs+tissues and blood) of 3.472 litres. At a depth of 19 m, the lungs will have been compressed from the volume of 14.156 litres at the surface to a volume of 4.881 litres. This latter figure therefore defines the lung volume that needs to be realized for the turtle to achieve neutral buoyancy. The volume of the lungs that needs to be attained after inspiration at the surface for the turtle to be neutrally buoyant (i.e. for the lungs to be compressed to 4.881 litres) at various depths is readily calculated, from which the lung oxygen store and hence the total oxygen store (lungs+tissues and blood) available at the start of the dive can be determined (Fig. 8). These calculations show how the total oxygen store increases with deeper dives because

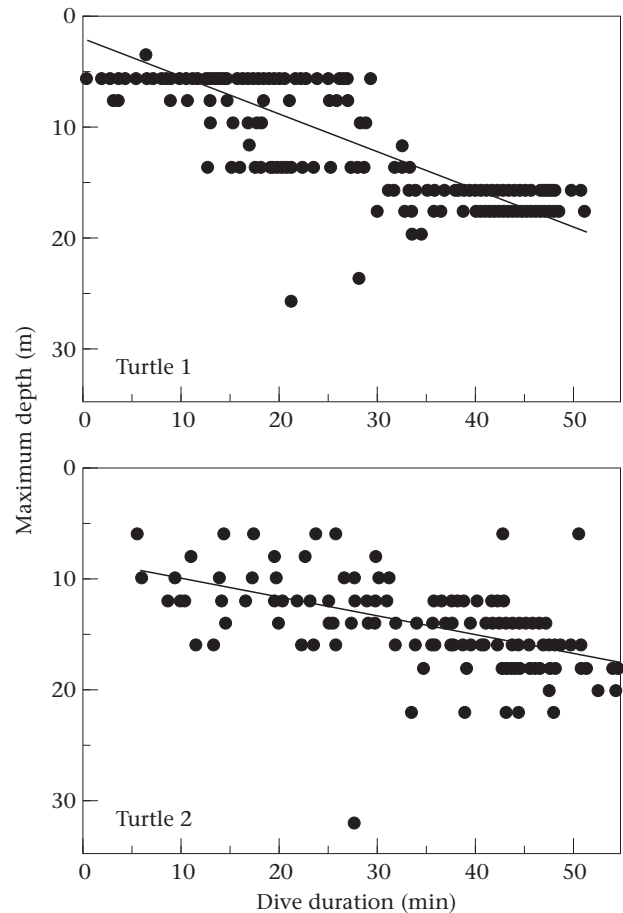


Figure 5. The relationship between the maximum depth of individual resting dives and their duration. Turtle 1: duration (min) = $3.08 + 2.10$ maximum depth (m); $F_{1,257} = 564$, $r^2 = 0.69$, $P < 0.001$. Turtle 2: duration (min) = $12.3 + 1.66$ maximum depth (m); $F_{1,163} = 59$, $r^2 = 0.27$, $P < 0.001$.

a larger inspiration can occur at the surface prior to the dive, until at a certain depth (19 m in this case) the maximal total oxygen store is attained.

We have empirically derived values for how the duration of resting dives varies with dive depth (Fig. 5). For example, for turtle 1 the mean dive duration increases from 15.7 to 36.7 min when dive depth increases from 6 to 16 m (Fig. 5), an increase of 21 min. The calculated increase in the total oxygen store going from 6 to 16 m is from 2.368 to 3.217 litres of oxygen (Fig. 8), an increase of 0.849 litres of oxygen. We can therefore infer that the extra 0.849 litres of oxygen available on the deeper dive sustains an extra 21 min dive duration and hence the estimated metabolic rate during the resting dive is 2.43 litres O_2 /h or 0.016 litres O_2 /kg per h.

With this metabolic rate, and with a total oxygen store of 3.472 litres, the maximum aerobic dive duration for turtle 1 would be 86 min. However, when this turtle conducted resting dives to 19 m the mean dive duration was only 43 min (using the regression equation in the legend to Fig. 5).

Similarly, we can repeat the calculations in exactly the same way for turtle 2 to derive a resting metabolic rate of

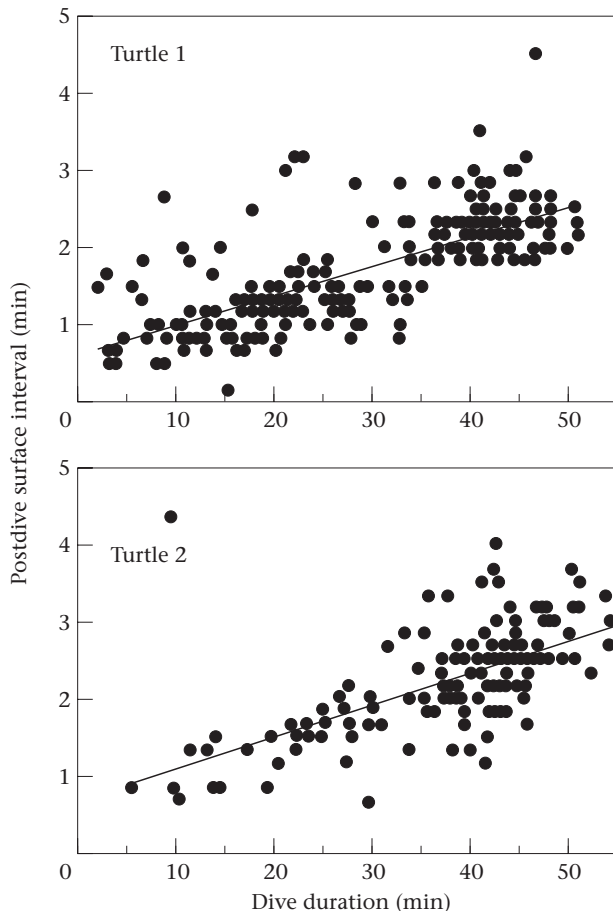


Figure 6. The relationship between dive duration and postdive surfacing interval. Turtle 1: surface interval (min) = $0.609 + 0.0384$ dive duration (min); $F_{1,233} = 274$, $r^2 = 0.54$, $P < 0.001$. Turtle 2: surfacing interval (min) = $0.674 + 0.0411$ dive duration (min); $F_{1,131} = 84$, $r^2 = 0.39$, $P < 0.001$.

4.813 litres O_2/h or 0.020 litres O_2/kg per h and a maximum aerobic dive duration at 19 m of 70 min compared to the mean observed (regression equation in the legend to Fig. 5) value of 44 min.

DISCUSSION

Time–depth recorders are now widely used to look at the diving behaviour of marine animals such as marine mammals, birds and reptiles (Schreer & Kovacs 1997; Pütz et al. 1998). Defining a depth at which dives are considered to start is somewhat arbitrary. We used a depth of 3 m as has been done elsewhere with TDRs of the type we used (Boveng et al. 1996). A constant challenge in these studies is to try to infer the behaviour of individuals from their diving records. For some groups, such as marine mammals, multivariate statistics have been used to diagnose different dive profiles statistically (Schreer & Testa 1995), although this still leaves open to question the types of behaviour being performed when the different profiles are conducted (Schreer & Testa 1996). For some marine turtle populations, the problem of interpreting TDR data is somewhat simplified because individuals are known to

spend inactive periods lying on the sea bed and this gives rise to a characteristic resting dive profile which has a flat bottom section separating the initial descent and final ascent. For example, for immature hawksbill turtles, *Eretmochelys imbricata*, in the Caribbean, van Dam & Diez (1996) noted flat-bottomed resting dive profiles, while, in contrast, the depth constantly changed when the turtles were foraging. They found a diel pattern in diving activity (as has also been noted more recently with adult hawksbills in the interinteresting period; Starbird et al. 1999) and noted that individuals rested for about 50–80% of the night while they were largely active during the day. While turtles in some areas may actively forage during the interinteresting period (e.g. Hochscheid et al. 1999), there is little food for green turtles around Ascension Island and hence they are not thought to feed (Carr et al. 1974). Hence flat-bottomed dive profiles for green turtles at Ascension Island are almost certainly always caused by turtles resting on the sea bed and indeed scuba divers have reported observing resting turtles.

We found that the resting dives of green turtles on Ascension Island were typically shallower than 30 m. This is consistent with the general view that green turtles, along with other species such as the loggerhead and hawksbill, are generally shallow divers that rely on their lungs as an important oxygen source during dives (Lutcavage & Lutz 1997). In contrast, the leatherback turtle, *Dermochelys coriacea*, relies far more on extensive oxygen stores in the blood and tissues. While this species sometimes conducts shallow dives (e.g. Southwood et al. 1999) it is frequently thought to be a deeper diver, in some areas routinely descending to more than 100 m during the interinteresting period and occasionally diving beyond 1000 m (Eckert et al. 1989). At Ascension, water depths of less than 30 m are found only within a few kilometres of the island and further offshore the sea bed rapidly shelves to depths of several hundred metres. The depth of resting dives therefore shows these turtles must have been close to the shore. This conclusion is supported by previous tracking studies that have shown that during the interinteresting period the turtles remain close to the island (Mortimer & Portier 1989).

In marine mammals, very long surface intervals generally occur after anaerobic dives. For example, a typical recovery time of about 60 min has been shown for Weddell seals, *Leptonychotes weddelli*, after dives of 40 min (Kooyman et al. 1980). This long recovery time is associated with the oxidization of accumulated lactate (Thompson & Fedak 1993). In contrast, the postdive surfacing intervals we observed for green turtles were always short, as would be expected after aerobic dives. The increase in the postdive surface duration that we noted after longer dives has also been shown for grey seals, *Halichoerus grypus*, diving aerobically (Thompson & Fedak 1993) and is presumably associated with the extra time required to replenish oxygen stores or to eliminate carbon dioxide after longer dives.

Resting dives were longer when the turtles dived deeper. This has also been noted for loggerhead turtles, prompting the suggestion that deeper dives are longer because the turtle is able to fill its lungs with more air

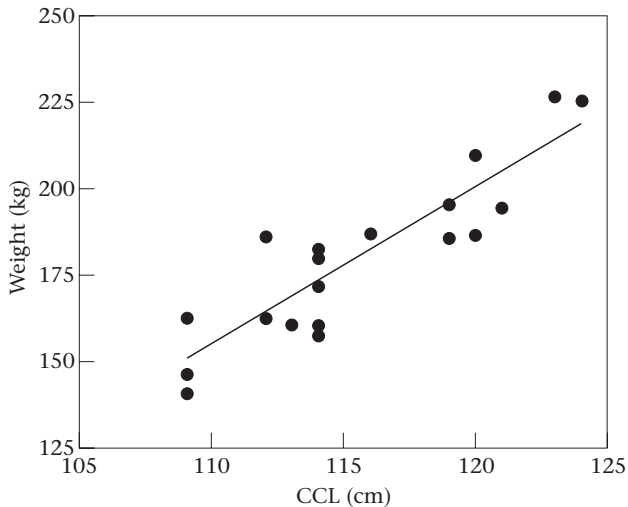


Figure 7. The relationship between the weight of nesting green turtles on Ascension Island and their curve carapace length (CCL). $\text{Weight (kg)} = 4.585 \text{ CCL} - 349.22$ ($F_{1,18} = 70$, $r^2 = 0.80$, $P < 0.001$). Each point represents data from a separate individual.

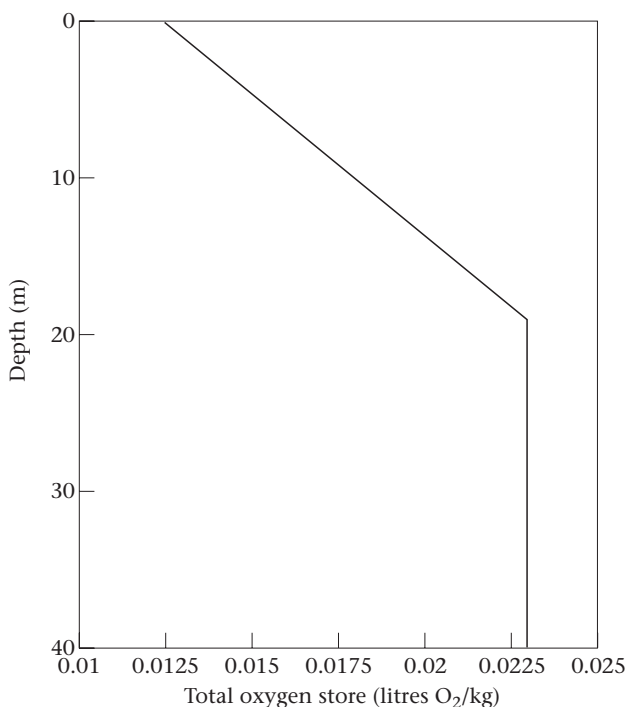


Figure 8. The total oxygen store for resting dives for turtle 1 assuming that at the resting depth the lungs would always be compressed to a volume of 4.881 litres for neutral buoyancy to be attained and that, after the turtle had inspired fully, neutral buoyancy would be attained at 19 m. The weight specific oxygen stores are identical when the calculations are repeated for turtle 2.

prior to the dive and still achieve neutral buoyancy at depth (Minamikawa et al. 1997). As such we used this relationship between dive depth and dive duration to estimate the oxygen stores that were available on dives to different depths and hence the metabolic rate of these turtles. Our model is based on realistic assumptions. We

have used literature values for the lung volume, the oxygen content of the lungs at the start of a dive and the oxygen carrying capacity of the blood and tissues. We assumed that the turtles' lungs are compressed in accordance with Boyle's Law, which has indeed been shown to be the case (Berkson 1967). Perhaps our most tenuous assumption is that 19 m was the depth at which neutral buoyancy was attained if the turtles inhaled fully before diving. This depth was selected because it corresponded to the maximum modal dive depth. Conceivably, however, the depth for negative buoyancy with a full inspiration might have been deeper. In effect this would mean that the turtles routinely did not inflate their lungs fully before a dive, even when going to their maximum resting depth. If this were the case, the implication is that we would have overestimated the metabolic rate of the turtles. For example, if the depth at which neutral buoyancy was attained had been 30 m (and not 19 m as assumed) then the calculated metabolic rates for the two turtles would have decreased from 0.016 and 0.020 litres O_2/kg per h, respectively, to 0.011 and 0.015 litres O_2/kg per h, respectively.

General support for the model is provided by the fact that it suggests that all resting dives are aerobic, which is thought to be the case for voluntary submergences by turtles (Lutz & Bentley 1985) and is consistent with the short postdive surfacing intervals we observed. More specific support comes from the fact that the model suggests that turtles typically use only about half of their available oxygen stores during resting dives. This value is consistent with the observation that during voluntary dives juvenile loggerhead turtles surface after only about 75% of the lung oxygen store and 50% of the blood and tissue oxygen store has been used (Lutcavage & Lutz 1991).

There are no estimates of the metabolic rate of turtles during resting dives with which to compare our values. Indeed, measurements of the metabolic rate of sea turtles while they are at sea are entirely lacking. For logistic reasons, previous studies on the energetics of marine turtles have focused on hatchlings (Wyneken 1997) or juveniles (Prange 1976; Butler et al. 1984) maintained in artificial tanks, or adults while they are on nesting beaches. For adults, metabolic rates are relatively high when individuals are engaged in strenuous activities such as covering the nest. For example, for leatherback turtles values of 0.222 litres O_2/kg per h have been measured for turtles covering the nest (Paladino et al. 1990). In comparison, a mean value of 0.015 litres O_2/kg per h was found for unrestrained leatherback turtles during egg laying (Lutcavage et al. 1990) and a minimum value of 0.024 litres O_2/kg per h was recorded for adult green turtles resting on land (Prange & Jackson 1976). These are both similar to our calculated metabolic rate for green turtles during resting dives (0.016 and 0.020 litres O_2/kg per h). Prange & Jackson (1976) synthesized available data for different-sized animals to show that the minimal mass-specific oxygen consumption of turtles decreased with increasing size, being described by the equation: oxygen consumption (litres O_2/kg per h) = $0.058 (\text{weight in kg})^{-0.174}$. This produces a predicted minimal

metabolic rate of 0.023 litres O₂/kg per h for a 200-kg turtle, again similar to our values. The implication is that the metabolic rate during resting dives is similar to both the minimal values recorded for quiescent turtles on land and the value predicted from the allometric scaling of metabolic rate.

We can therefore examine, with confidence, the use of energy reserves that would be needed to sustain turtles at Ascension Island during the internesting period. The modal interval between consecutive nests by these turtles is 13 days (Mortimer & Carr 1987). If we assume that turtles spend, on average, 40% of this time resting, during which time their oxygen consumption is 0.018 litres O₂/kg per h (the mean value from our study), and that they metabolize fat from which the energy derived is 39.31 kJ/g (Schmidt-Nielsen 1990), then over 13 days the 150.6-kg and 236.5-kg turtles would expend 6651 and 10 444 kJ, respectively, during resting dives, using 169 and 266 g of fat, respectively. The relative importance of these values can be gauged by considering the energy content of turtle eggs. Green turtle eggs laid at Tortuguero, Costa Rica, have a mean diameter of 44.4 mm (Bjorndal & Carr 1989) and a mean energy content of 259.7 kJ per egg (Bjorndal 1982). Green turtle eggs laid on Ascension Island have a mean diameter of 45.5 mm (Hays et al. 1993) and, assuming that their volume-specific energy content is the same as for eggs in Costa Rica, then their mean energy content is 279.5 kJ. If we estimate that the metabolic rate of green turtles trebles between resting dives and dives in which they are active during the internesting period, then the energy saved by the two turtles by resting for 40% of the time during the internesting period would be 13 302 and 20 888 kJ, equating to the energy content of 48 and 75 eggs, respectively.

These calculations suggest that by spending long periods resting between successive nesting emergences, green turtles at Ascension Island will reduce their energy expenditure during the internesting period by ecologically significant amounts, allowing them to increase their investment in the number and/or quality of the eggs that they lay.

Acknowledgments

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