Body Mass and the Energy Budget of Gravid Hawksbill Turtles (*Eretmochelys imbricata*) during the Nesting Season

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ABSTRACT.—Female Hawksbill Turtles (*Eretmochelys imbricata*) nesting along the southeast coastline of the state of Rio Grande do Norte Brazil (6°13′40″S, 35°03′05″W) were captured and weighed during the 2006–07 and 2007–08 nesting seasons. The mean value for the first postoviposition mass was 79.6 kg. Individuals that were subsequently recaptured showed a mean mass change of 1.6 kg in the interval between two consecutive postovipositions (i.e., after one internidal interval). We plotted the mass of the individuals against the curvilinear carapace length. An analysis of residual mass above average body condition reveals that females with good body condition start nesting at the beginning of the season. Preoviposition mass was measured when the female aborted the nesting process. Gross mass change was 5.46 kg. Mean body mass recovery was 3.2 kg. Body mass recovery was always significantly lower than the change in gross mass. This is in agreement with the observed mass loss tendency throughout the breeding season for this species. Mass recovery was analyzed using allometric law, converting both loss in body mass and total egg mass to energy. Using mean turtle body mass, we performed three scenarios for the metabolic maintenance rate of the Hawksbill Turtle during the nesting period. The energy that the turtles expended in egg laying was estimated at 1,183 kJ · d^{-1}. The daily net mass loss for the most realistic scenario converted into energy was 4,213 kJ · d^{-1}. The total daily energy consumption (maintenance plus egg production) was similar to the daily energy from mass loss. This theoretical treatment suggests that, under this scenario, there is no reason for significant extra energy intake during the oviposition period.

As with all adult female marine turtles, the Hawksbill Turtle (*Eretmochelys imbricata*) must build up energy in foraging areas in preparation for reproduction, usually spending several years foraging before migrating to the breeding sites (Bjorndal, 1995). The stored energy is used in both the process of vitellogenesis and migration to and from the nesting area, often hundreds of miles away (Starbird et al., 1999; Troeng et al., 2005). Despite the dearth of information concerning the Hawksbill Turtle's energy strategies, it is hypothesized that, similar to other turtle species, energy storage occurs mainly through the formation of fat reserves (Kwan, 1994; Hamann et al., 2002).

Like most other marine turtles, the Hawksbill Turtle is iteroparous within each nesting season and is able to lay between one and eight clutches during a single egg-laying period (Chan and Liew, 1999; Dobbs et al., 1999). The low estimates for clutch frequency in the published literature (e.g., Loop et al., 1995; Al-Merghani, 2000) could possibly reflect incomplete coverage (Dobbs et al., 1999). Meticulous surveys indicate between four and five clutches per individual during each nesting season (Richardson et al., 2006). According to the literature, the intervals between one successful nesting event and another vary from 10–20 days, the average being 15 days (Mortimer and Bresson, 1999). Intervals of less than seven days are taken to signify incomplete oviposition (divided laying), whereas intervals of more than 23 days are assumed to result from unobserved nesting events (Mortimer and Bresson, 1999). The interval between successive breeding seasons for a determinate individual is usually from 2–3 yr (Richardson et al., 2006) but can vary from nine months (Pilcher and Ali, 1999) to seven years (Mortimer and Bresson, 1999).

Female sea turtles, as long-lived iteroparous animals, can skip reproduction if they do not have sufficient fat reserves (Broderick et al., 2001; Hatase and Tskamoto, 2008). This situation leads to a variety of remigration intervals

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within a population, whereby individuals who skip reproduction continue to feed, allowing them to accumulate fat reserves for a longer period (Hays, 2000; Hatase and Tskamoto, 2008).

The energy budget concept furnishes a standard framework for the comparison of metabolic processes, including mass loss and gain, oviposition, and the cycle of energy building and consumption in everyday life. Here, we use the concept to analyze changes in the body mass of *E. imbricata* during the nesting period from the perspective of the individual's energy budget. Successive preoviposition and postoviposition mass measurements enabled us to calculate the available energy. Moreover, using previous results from the literature and taking egg mass measurements, we estimated the energy cost of oviposition under different scenarios for the metabolic rate of the species to make a comparison with our results.

The estimate of the energy budget of Hawksbill Turtles is used in this article to clarify the issue of mass recovery during the oviposition period. Although this species recovers mass between two successive ovipositions, it is not clear whether there is any energy intake during the period or whether the mass gain is caused by rehydration.

In this paper, we test the hypothesis that gravid Hawksbill Turtles do not feed during the nesting period; rather, they rely entirely on their energy reserves for their reproductive activity. To accomplish this, we evaluated energy expenditure using theoretical analyses under different scenarios. If energy consumption during oviposition is greater than the available stored energy, it would indicate that a turtle must have another source of energy; that is, the turtle would have to eat during the nesting season to balance energy input and output. Even though the theoretical analysis is not conclusive, we believe that these assays may contribute to answering these questions.

MATERIAL AND METHODS

Characterization of the Area.—The beach area monitored is approximately 4 km in length, situated in the southern section of the coastline of Tibau do Sul in the state of Rio Grande do Norte (6°13′40″S; 35°03′05″W), approximately 80 km south of the city of Natal. It consists of Cancela, Minas, and Sibauma beaches. The landscape is composed of cliffs interspersed with dunes, exposing a narrow band of beach.

Data Collection.—During the nesting seasons of 2006–07 and 2007–08, we undertook intensive night-long patrols from 1900–0430 h to intercept and mark nesting females. The intercepted females were marked with inconel metal tags (number 681 National Band and Tag Company), applied close to the most proximal scale at the axillary region of both front flippers.

The curved carapace length (CCL) of all intercepted females was measured with a flexible measuring tape between the external border of the nuchal scale and the external border of the supracaudal scale to within 0.1 cm (Marcovaldi and Marcovaldi, 1999).

We intercepted and weighed individuals on the beach after the turtle had concluded its nesting attempt (successful or not). We brushed off all sand from the turtle and then placed it on a stretcher attached to a digital scale that was suspended from a metal frame. The accuracy of the scales (Filizola, maximum capacity of 500 kg, with a precision of ±100 g) was calibrated using objects of known weight before the start and throughout data collection.

Egg mass was measured using a Pesola spring balance (capacity = 50 g and precision of ±0.5 g). The accuracy of the spring balance was calibrated using objects of known weight, before the start and over the course of data collection. Eggs were collected in a plastic bag at the moment of laying, avoiding the adhesion of sand. A plastic cup, whose mass was subtracted from the total mass, was used to suspend the egg from the scale. This procedure was performed at the end of the 2007–08 nesting season on five nests. All the eggs in one nest were weighed, and an average of 25 eggs in the others was randomly selected. After being weighed, all the eggs were placed into the nest.

Approximately 45 days after laying, nests were checked for emergence, manifested by the presence of hatchling tracks or by a depression in the sand above the egg chamber. Nests were excavated 24 h after emergence to count clutch size. Clutch size was defined as the sum of dead hatchlings with their egg-shells, unopened eggs, and empty eggshells.

Data Processing.—The CCL with barnacles as interference were excluded from the analysis. The residual value from the first postoviposition mass versus CCL was plotted against day 0 of the nesting season. Thus, we tested whether females arriving later had different body condition.

The mass measurement immediately after laying was termed ''postoviposition mass.'' In rare cases in which the female crawled up the beach but did not nest, we were able to record the mass of the females before oviposition; this measurement was termed ''preoviposition mass.'' The internidal interval was defined as the number of complete days (24 h) between the

egg-laying night and the subsequent egg-laying night. Data points whose intervals were longer than 23 days were excluded from the analyses. When the interval between two mass measurements was greater than 23 days, it was attributed to unobserved nesting events.

The difference between two consecutive postovipositions was termed "net mass change." The difference between preoviposition mass and the related postoviposition mass (separated by a maximum time interval of three days) was called "gross mass change" (encompassing clutch mass plus other changes in gross body mass resulting from alterations in the degree of tissue hydration, depletion of fat reserves, etc.). The three-day interval was chosen because of the authors' prior experience in the field, showing that this is the maximum period for a turtle to return after an unsuccessful attempt. The difference in mass between one postoviposition and the subsequent preoviposition is the "mass recovery." This measurement is typically carried out over an interval comparable to the internidal interval, because even when the turtle did not nest, we assumed that there was reproductive intention even though the attempt was unsuccessful. In such cases, the term "potential internidal interval" was used.

Mean egg mass was calculated by taking the mean of all egg mass measurements from the five different females. Mean clutch mass for the population was obtained by multiplying average unit egg mass by mean clutch size.

Daily mass recovery was calculated as the difference in mass between one postoviposition and successive preoviposition mass divided by the potential internidal interval. This procedure was carried out only for females with known preoviposition mass. We divided the net mass change by the average internidal interval in days to obtain an estimation of daily net mass change during the internidal interval. Although the mass loss occurs mainly just after egg laying and not throughout the entire internidal interval, we performed this procedure to obtain daily values and facilitate comparison.

Total gross mass loss during the entire nesting season was calculated through the difference between the initial mass (first preoviposition mass) and the postoviposition mass observed in the last laying. In cases where the first preoviposition mass was not observed, it was estimated by adding the percentage of gross mass change to the first postoviposition mass. Means are given ±1 SD.

Theoretical Treatment.—There are two main energy consumption demands for a marine turtle during the oviposition period: the energy expended in egg production and metabolic maintenance energy. The latter includes the energy used in all metabolic processes (breathing, locomotion, excretion, sensing, nest digging, etc.).

We assume that the energetic value for eggs per gram is the same for Loggerhead (*Caretta caretta*) and Hawksbill Turtles. Bouchard and Bjorndal (2000) report that each Loggerhead Turtle egg contains 171.21 kJ of energy. The mean wet mass of the *C. caretta* eggs was 39.8 g (S. Bouchard, pers. comm.). Dividing the energy value by the wet mass gives energy value per gram of $4.2 \text{ kJ} \cdot \text{g}^{-1}$.

The energy content of a clutch was calculated using energy per gram of egg and clutch mass. To compare this energy content with metabolic rate, we divided it by the mean internidal interval. Although the energy expended in a clutch is mainly concentrated in egg laying, we estimated this amount daily for a numerical comparison. In addition, we observed that the mass change (between two postovipositions) and the time interval (internidal interval) are consistent measurements in the sense that both are related to the same period of time.

To estimate the metabolic rate of *E. imbricata*, we used allometric reasoning. Wallace and Jones (2008), in a review of marine turtle metabolic rates, concluded that allometric relationships between metabolic rate and body mass are constant for Leatherback Turtles (*Dermochelys coriacea*), Green Turtles (*Chelonia mydas*), and other reptiles. Under allometric theory, the metabolic rate M is expressed as a function of mass m according to the relation $M = c\, m^a$, where c and a are constants empirically derived from a large set of animals within the same class. We consider two distinct methodologies to estimate this amount: the basal metabolic rate (BMR) according to Schmidt-Nielsen (1984); and the field metabolic rate (FMR) as reviewed in Nagy (2005). In both cases, we use the reptile allometric scale. For BMR, we have the relationship $M = 32.6\, m^{0.83}$ and, for FMR, $M = 91.1\, m^{0.89}$ (in both equations the mass is expressed in kilograms and the metabolic rate in $\text{kJ} \cdot \text{d}^{-1}$). BMR measures minimum maintenance energy consumption, whereas FMR measures field activity, which takes into account the energy expended in locomotion and other activities, such as nest digging. We constructed three different hypothetical scenarios to estimate the metabolic maintenance rate during the nesting period: (1) minimal energy cost, which only takes into account BMR; (2) maximum energy cost, which only takes into account FMR; and (3) medium energy cost, which takes into account the average between BMR and FMR.

An energy budget is summarized by energy input–energy output. The energy input (source) of *E. imbricata* during oviposition is basically the

TABLE 1.   Body mass of nesting Hawksbill Turtles according to ocean and country.

Location	Mean (kg)	Range (kg)	N	SD (kg)	Stage	Source
Atlantic Ocean						
Nicaragua	54.2	27.2–86.2	32	–	–	Nietschmann, 1972[a]
Puerto Rico	68.4	60.5–76.3	2	–	–	Thurston and Wiewandt, 1976[a]
Barbados	68.2	44–92	68	8.8	postoviposition	Beggs et al., 2007
Pipa, Brazil	86.0	60.1–112.2	75	11.8	first preoviposition	This study
Pipa, Brazil	79.6	56.2–105.7	72	11.3	first postoviposition	This study
Pacific Ocean						
Solomon Islands	66.3	41.8–77.3	40	–	–	McKeown, 1977[a]
Solomon Islands	57.8	36.0–72.5	43	–	–	Vaughan, 1981[a]
Australia	49.5	45.5–55.0	8	–	–	Limpus, 1980[a]
Campbell Island, Australia	51.6	38.5–68.0	38	8.22	postoviposition	Limpus et al., 1983
Milman Island, Australia	50.4	32.0–72.0	582	6.45	postoviposition	Dobbs et al., 1999
Indian Ocean						
Democratic Yemen	43.2	35.3–50.0	15	–	–	Hirth and Carr 1970[a]
Seychelles	65.6	51.2–83	75	8.11	first preoviposition	Hitchins et al., 2004
Seychelles	60.9	48.0–79.0	74	7.89	first postoviposition	Hitchins et al., 2004
Islands of Persian Gulf	39.2	10.0–64.0	123	6.7	–	Pilcher, 1999
Kingdon of Saudi Arabia	38.2	26.0–64.0	245	5.96	postoviposition	Al-Merghani et al., 2000
Arabian Gulf	39.1	26.0–64.0	175	6.32	postoviposition	Al-Merghani et al., 1996
Saudi Arabia	38.4	30.5–40.0	–	–	–	Miller, 1989

[a] Sources cited in Witzell (1983).

consumption of energy reserves (usually fat) plus possible feeding. Output (waste energy) is related to oviposition and the usual metabolic consumption. We evaluate the stored energy expended through the measured mean mass change multiplied by the food energy (in kJ) of fat.

RESULTS

Biometric Analysis.—We took 182 mass measurements on 76 nesting Hawksbill Turtles within the study area on the southern coastline of Rio Grande do Norte during the 2006–07 and 2007–08 nesting seasons. On first contact, the females exhibited an average postoviposition mass of 79.6 ± 11.3 kg (range, 56.2–105.7 kg; N = 72; Table 1). The average first preoviposition mass was estimated at 86.0 ± 11.8 kg (range, 60.1–112.2 kg; N = 75; Table 1). When first preoviposition mass was not available, we estimated this value by adding the gross mass change (6.9%) to the first postoviposition mass.

Of 72 turtles with available postoviposition mass, 18 individuals had barnacles as interference on CCL and were excluded from the analysis. The average CCL was 0.92 ± 0.04 m (range, 0.83–1.01 m; N = 54), and mass increased proportionally (Fig. 1). In addition, we plotted the residual of the mass value against day 0 in the nesting season (Fig. 2), where day 0 means the day when the night-long patrols started and was

10 December for both nesting seasons, 2006–07 and 2007–08. There was a significant relationship (P = 0.0118) between female body condition and day of the season (Fig. 2), but only 11.6% of the variation was explained.

Individuals that were subsequently recaptured showed a mean mass change of 1.6 ± 1.43 kg (range, −3.7–5.1; N = 75 sets of measurements on 36 females) in the interval between two consecutive postovipositions, separated by a maximum time interval of 18 days, indicating an average mass change of 2.0% (Fig. 3, Table 2). Within the 75 measurements, we observed mass gains in eight measurements and no changes in two measurements. Consid-
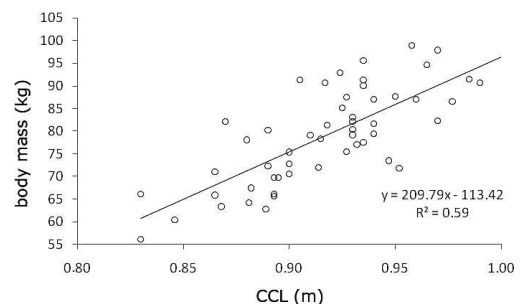

FIG. 1.   Relationship between the first postoviposition mass of nesting Hawkbill Turtles (*Eretmochelys imbricata*) and their curved carapace length (CCL) on the southeast coast of Rio Grande do Norte, Brazil.
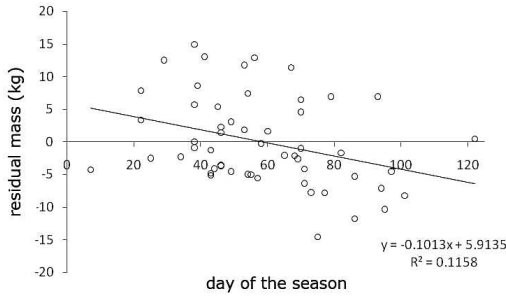
FIG. 2.   Residual mass against the day of the nesting season, where day 0 is 10 December 2006 for the 2006–07 nesting season and 10 December 2007 for the 2007–08 nesting season. Positive values indicate individuals with body condition above average and negative values for individuals below the average. The correlation reveals that females with body condition above average start nesting at the beginning of the nesting season.

ering the entire season, only two of 36 females gained mass. However, these two exceptional females were observed nesting only twice. All females that nested at least three times always lost mass in the course of the entire season.

Mean gross mass change was 5.5 ± 1.09 kg (range 4.3–8.2; $N = 12$ sets of measurements), indicating an average mass loss of 6.9% (Fig. 4). This value was significantly higher (t-test, $P < 0.001$; $t = 9.03$; df = 85) than the loss between two consecutive postoviposition measurements from the same female. This finding points to considerable mass recovery, reflecting the development of a new egg mass within the female.

Mean body mass recovery was 3.2 ± 1.05 kg (range 1.8–4.6; $N = 9$ sets of measurements), indicating an average mass recovery of 4.3% during the potential internidal interval (Fig. 4). Although the sample size is small, the recovery in body mass was always significantly lower (t-test, $P < 0.005$; $t = 4.69$; df = 18) than the gross mass change. This finding is in agreement with the observed mass loss tendency throughout the breeding season in this study.

Average clutch size was 143 ± 27.6 eggs per nest (range 41–207; $N = 83$), and average egg mass
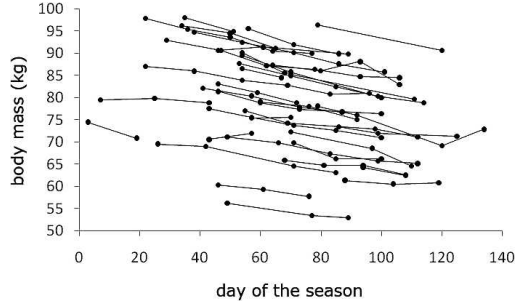

FIG. 3.   Postoviposition mass for 36 nesting Hawksbill Turtles weighed more than once on the southeast coast of the state of Rio Grande do Norte, Brazil. Each line joining the postoviposition mass represents the net mass change for the same individual. Day 0 on the x-axis for the 2006–07 and 2007–08 nesting seasons was 10 December in both 2006 and 2007.

was 29.0 ± 2.46 g (range 19.3–32.2; $N = 251$). The average clutch mass was estimated at 4,147 g.

The average internidal interval for the 36 individuals weighed more than once was 14.72 ± 1.4 days (range 12–18; $N = 75$). Average mass recovery on a daily basis during the potential internidal interval was 0.23 ± 0.08 kg $\cdot$ d^{-1} (range 0.13–0.35 kg $\cdot$ d^{-1}; $N = 9$). Dividing the difference between two consecutive postoviposition mass measurements by the internidal interval, we have a daily average net mass loss of 0.112 ± 0.1 kg $\cdot$ d^{-1}, (range −0.264 to 0.392 kg $\cdot$ d^{-1}; $N = 75$).

Theoretical Estimations.—The average mass change (loss) during two consecutive postovipositions is 0.112 kg $\cdot$ d^{-1}. Considering that mass loss is caused by fat consumption (energetic value 37.6 kJ $\cdot$ g^{-1}; Schmidt-Nielsen, 1983), the average estimated energy expenditure during the internidal interval is 4,213 kJ $\cdot$ d^{-1}. The caloric egg content of *E. imbricata* is around 4.2 kJ $\cdot$ g^{-1}. Our estimation for the total egg mass in a clutch is 4,147 g. Therefore, the total energy content of a clutch is 17,417.4 kJ, which translates into an average egg energy investment of 1,183 kJ $\cdot$ d^{-1}.

An assumption in our calculations is that the observed reduction in mass is caused by fat metabolism. However, many vertebrates com-

TABLE 2.   Difference between postoviposition mass (net mass changes) for two to six consecutive ovipositions of the 36 nesting Hawksbill Turtles weighed more than once during the 2006–07 and 2007–08 nesting seasons, on the southeast coast of the state of Rio Grande do Norte, Brazil. Negative values indicate mass gain.

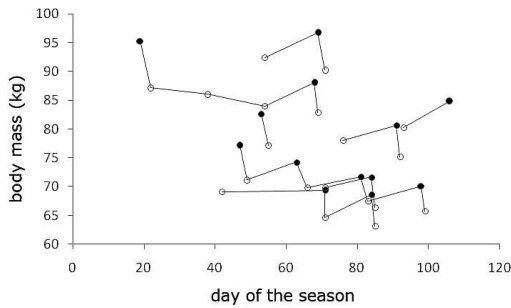| Nests between	Mean (kg)	SD (kg)	N	Range (kg)	%
Two consecutive	1.6	1.4	75	−3.7 to 5.1	2.0
First and third	3.4	1.8	21	−0.8 to 5.7	4.2
First and fourth	5.4	2.2	20	0.9–9.5	6.6
First and fifth	6.8	1.6	11	5.0–8.9	8.2
First and sixth	7.2	1.4	2	6.1–8.4	8.0

FIG. 4. Loss or recovery of body mass for eight nesting Hawksbill Turtles on the southeast coast of the state of Rio Grande do Norte, Brazil. The blank circles represent postoviposition mass, and the solid circles represent preoviposition mass. Each line joins mass measurements for the same individual. Gross mass change in kilograms (loss) is represented by the line joining preoviposition mass to the successive postoviposition mass. Mass gain (mass recovery) during the (potential) internidal interval is represented by the lines joining postoviposition mass to the successive preoviposition mass. The abrupt mass loss (gross mass change) is caused by oviposition, and the slow gain corresponds to rehydration in the internidal interval. Day 0 on the x-axis for the 2006–07 and 2007–08 nesting seasons was 10 December in both 2006 and 2007.

monly consume both fat and protein during fasting periods (Schmidt-Nielsen, 1983). The energy content of protein is 17 kJ · g^{-1}, and if all the mass loss of the turtle was caused by protein metabolism, the metabolic rate would be 1,670 kJ · d^{-1}. Therefore, our fat based estimation of 4,213 kJ · d^{-1} should be considered an upper metabolic rate limit.

Metabolic rate was computed using the average mass m = 79.6 kg. The results are as follows: (1) BMR = 1,230 kJ · d^{-1} representing minimum energy requirement; (2) FMR = 4,480 kJ · d^{-1} representing maximum energy requirement; (3) average between BMR and FMR = 2,870 kJ · d^{-1} representing mean energy requirement.

DISCUSSION

Few studies have evaluated the change in body mass of sea turtles during the nesting season. Because there is a significant difference between preoviposition and postoviposition mass, and given the tendency to lose mass after successive layings, it is imperative that the calculation of the average mass of the population take into account the reproductive stage in which the turtle was found. The average mass (pre- and postovipositions) of the nesting Hawksbill Turtles along the southern coastline of Rio Grande do Norte is the highest ever reported for this species worldwide (Table 1). As expected, the average unit egg mass is also

higher than that reported from other regions (e.g., 26.6 g; Miller, 1996).

The preoviposition mass was determined for this species in the Seychelles Islands (Hitchins et al., 2004) by adding egg mass to postoviposition mass, whereas our figure was obtained by weighing the gravid female when possible or by adding 6.9%, which represents the average change in gross mass, to the postoviposition mass. Thus, our measurements take into account the loss of liquid and nutritional reserves associated to the nesting process, raising the accuracy to register mass changes.

We estimate that a reproductive Hawksbill Turtle that lays three to five clutches within a season usually will lose 11.1–15.1% of its initial preoviposition mass. Hitchins et al. (2004) argued that a nesting Hawksbill Turtle can lose 8.5–15.4% of its initial preoviposition mass after laying three to five times, but Dobbs et al. (1999) did not find significant mass loss for Hawksbill females that nested from three to five times within the same season. The Leatherback maintains practically the same mass after consecutive ovipositions within a season, suggesting that they feed during this period (Eckert et al., 1989; see also Myers and Hays, 2006). Hays et al. (2002) estimated the average rate of mass loss in Green Turtles on Ascension Island after successive postoviposition to be 0.22 kg · d^{-1} and, after analyzing the stomach contents of four individuals found dead, presumed that they did not feed during the nesting season. Our result for average internesting mass loss of a Hawksbill Turtle was 0.112 kg · d^{-1}. This difference between species appears to be inconsistent with allometric theory, which suggests smaller organisms have higher energetic consumption per mass than larger ones (Schmidt-Nielsen, 1984): the average mass for Green Turtles on Ascension Island is 166 kg (Hays et al., 2002), whereas we found the average mass of Hawksbill Turtles in Brazil was 79.6 kg. This difference may reflect variation in feeding behavior of marine turtle species or populations during the internesting period. For Green Turtles nesting at Ascension, no evidence of foraging of animals between nests was found (Carr et al., 1974; Hays et al., 2000). At Raine Island in Australia, however, between 30% and 50% of nesting female Green Turtles examined showed signs of recent feeding (Tucker and Read, 2001). Whether nesting Hawksbill Turtles in Brazil are foraging during the internesting period is currently unknown, as is nearby food availability.

Assuming that there was no mass recovery during the internidal interval, we estimate a female Hawksbill Turtle that nests from 3–5 times would lose from 20.7–34.5% of its initial preoviposition mass. Making a similar assumption, Hitchins et al.

(2004) estimated that *E. imbricata* would lose more than 36% of its initial mass, although they do not provide figures for the recovery. Taking into account our estimate of 1,183 kJ • d^{-1} required for clutch production during the internesting interval of our study population, we calculated the overall energy expenditures based on our theoretical minimum, maximum, and mean estimated energy requirements. For a Hawksbill turtle that weighs 79.6 kg, the estimated overall energy required for reproduction ranged from 2,413 kJ • d^{-1} (minimum), 5,663 kJ • d^{-1} (maximum), and 4,053 kJ • d^{-1} (average). The minimum value likely underestimates the energy cost because it does not take into account the energy expended while the nesting turtles ascend the beach or dig their nests. The maximum value assumes that fasting during the nesting period is not occurring; although it is possible, it is not consistent with broadly accepted assumptions of little to no food intake during the nesting period (Eckert et al., 1989; Reina et al., 2005; Myers and Hays, 2006; Houghton et al., 2008). Interestingly, the average value is similar to the estimated energy consumption required during the internesting interval (4,213 kJ • d^{-1}). Assuming the average value is correct, this would suggest that no significant extra energy intake takes place during the oviposition period but rather that mass recovery is caused by rehydration alone.

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