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Leatherback Turtles Are Capital Breeders: Morphometric and Physiological Evidence from Longitudinal Monitoring

Virginie Plot*
Thomas Jenkins
Jean-Patrice Robin
Sabrina Fossette†
Jean-Yves Georges
Université de Strasbourg, Institut Pluridisciplinaire Hubert Curien, 23 rue Becquerel, 67087 Strasbourg, France, and Centre National de la Recherche Scientifique, Unité Mixte de Recherche 7178, 67087 Strasbourg, France

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ABSTRACT

Organisms compensate for reproduction costs through two major strategies: capital breeders store body reserves before reproduction and do not feed during the breeding season, whereas income breeders adjust their food intake depending on concurrent reproductive needs. Sea turtles are commonly considered capital breeders. Yet recent biometric and behavioral studies have suggested that sea turtles may in fact feed during reproduction. We tested this hypothesis in the leatherback turtle *Dermochelys coriacea*, nesting in French Guiana. Our study is based on the innovative use of longitudinal monitoring for morphological (body size, body mass, and body condition) and physiological (plasma glucose, triacylglycerides, urea, calcium, and hematocrit) measurements in 35 females throughout the 2006 nesting season. During their 71-d nesting period, leatherbacks lost a mean (±SE) of 46.8 ± 2.6 kg (i.e., ~11% of their initial body mass of 409.0 ± 8.9 kg). Simultaneously, a significant decrease in plasma concentrations of glucose, triacylglycerides, and urea was observed throughout the nesting season, following typical patterns reported in other long-fasting animals that rely on lipid body stores. At the end of the nesting season, the interindividual variability in plasma concentrations was very low, which may characterize some minimum thresholds associated with the end of reproduction. We also identified a minimum necessary threshold for female body condition at the onset of reproduction; the body condition of any females beginning the nesting period below this threshold decreased dramatically. This study makes a compelling case that, in French Guiana, gravid leatherback females are anorexic during the nesting season (i.e., leatherback turtles are capital breeders). We further highlight the mechanisms that prevent this multiparous reptile from jeopardizing its own body condition while not feeding during reproduction.

* Corresponding author; e-mail: virginie.plot@iphc.cnrs.fr.
† Present address: National Oceanic and Atmospheric Association Southwest Fisheries Science Center, Environmental Research Division, Pacific Grove, California 93950.

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Introduction

Organisms exploit their environment to ensure survival, maintenance, growth, and reproduction and ultimately to maximize their fitness (Stearns 1992). However, the temporal and spatial fluctuations in resources that are inherent to a heterogeneous natural environment can entail variable periods of food deprivation for organisms (Mrosovsky and Sherry 1980). Organisms thus face trade-offs between competing life functions and compensate for this by adopting adaptative strategies at different levels (i.e., physiological, morphological, behavioral, and ecological) to ensure an optimal balance between energy acquisition and expenditure (Le Maho 2002).

Reproduction is generally considered to be an energetically highly costly life function. Organisms compensate for reproduction expenses by increasing trophic resource quantities through two different strategies: capital breeders store large quantities of body reserves before reproduction and then cease feeding during the reproductive episode, and income breeders adjust food intake during reproduction (Drent and Daan 1980; Jönsson 1997). In the wild, some species complement previously stored body reserves by feeding during the reproductive season. This type of intermediate strategy has been suggested in mammals (Wheatley et al. 2008), birds (Drent and Daan 1980; Sénéchal et al. 2011), and reptiles (Lourdais et al. 2002; Fossette et al. 2008*a*; Warner et al. 2008).

Sea turtles are commonly considered capital breeders (sensu Drent and Daan 1980), with females relying on body reserves stored during the preceding migration and ceasing to feed during reproduction (Miller 1997). However, recent morphometric (body mass change) and behavioral (diving and mouth-opening patterns and esophageal temperature) studies have contradicted this assertion in four of the seven sea turtle species. Opportunistic feeding during the reproductive season has already been suggested in green turtles *Chelonia mydas* (Hochscheid et al. 1999), hawksbill turtles *Eretmochelys imbricata* (Santos et al. 2010), loggerhead turtles *Caretta caretta* (Schoefield et al. 2006), and leatherback turtles *Dermochelys coriacea* (Southwood et al. 2005; Fossette et al. 2008*a*; Casey et al. 2010).

At the physiological level, organisms adapt to food resource deprivation by using the supply-side strategy (McCue 2007*a*). The supply-side strategy results in successive specific metabolic pathways of body reserve mobilization. It has been extensively described in endotherms (birds [Groscolas 1986; Cherel et al. 1988; Robin et al. 1998], mammals [Arnould and Rawlins 2001; Guinet et al. 2004]) and consists of three consecutive phases (Cherel et al. 1988). At the onset of the fast (phase I), postprandial animals enter a period of adaptation characterized by the exhaustion of glycogen stores and the progressive mobilization of lipid stores. As fasting continues (phase II), fat stores are preferentially mobilized, and low use is made of body proteins. Beyond a critical level of fat store depletion, long-fasting animals enter a critical phase (phase III) in which body proteins are increasingly catabolized. Recent studies on fasting ectotherms report similar patterns, with snakes chiefly relying on lipid stores while sparing proteins (McCue 2007*a*, 2007*b*, 2008). Investigating metabolic pathways during the reproduction period could therefore be a valid new approach to assessing the reproductive strategy (i.e., income vs. capital strategy) used by sea turtles.

Reproduction in sea turtles is energetically costly, because adult females come ashore regularly during the nesting season (which lasts several weeks) to lay successive clutches of several dozen eggs, with some interspecific differences (i.e., ranging from 50 eggs per clutch in the flatback turtle *Natator depressus* to 130 in the hawksbill turtles; Miller 1997). This high reproductive output most likely relies exclusively on previously stored maternal body reserves (Miller 1997). Surprisingly, few studies have investigated the metabolic adjustments in nesting sea turtles, probably because of constraints in performing longitudinal monitoring in the field (Hamann et al. 2002; Honarvar et al. 2011). Only a few studies on captive sea turtles have reported changes in plasma metabolites during periods of food deprivation (marginally shorter than during natural fasting in the wild; Bonnet 1979; Moon et al. 1999). Hamann et al. (2002) showed patterns of plasma triacylglycerides (TG) and total proteins during the nesting season in green turtles and concluded that nesting females chiefly rely on lipid stores and may shift to protein catabolism at the end of the season. In the leatherback, Honarvar et al. (2011) reported a decrease in plasma proteins as the season proceeds. Although some recent studies have reported plasma metabolite levels in leatherbacks when nesting or on foraging sites, these results were not interpreted in terms of fasting physiology, because they were based on transversal monitoring (Innis et al. 2010; Harris et al. 2011).

The leatherback turtle is the largest sea turtle species; the average adult leatherback female weighs between 250 and 400 kg, depending on the nesting population (Georges and Fossette 2006). This species shows the highest reproductive effort among sea turtles. Females lay an average of 6 clutches per season, with differences between nesting sites (Miller 1997) and between individuals (from 2 to 14 clutches per season; Eckert et al. 2012). During a nesting season that may last up to 3 mo, leatherbacks lay successive clutches about 10 d apart. This period is defined as the internesting interval (Miller 1997).

In French Guiana, where nesting leatherbacks are larger and heavier (Georges and Fossette 2006) and lay more clutches (Girondot and Fretey 1996) compared with other sites, females have been shown to disperse actively and extensively over the continental shelf during internesting intervals (Fossette et al. 2007; Georges et al. 2007). Clear patterns of mouth-opening at depth on the Guianese continental shelf have also been reported (Fossette et al. 2008*a*). In addition, the occurrence of jellyfish, which are the main prey of leatherbacks, has been reported in the vicinity of these nesting beaches (Fossette et al. 2009). These findings led to the hypothesis that leatherbacks in French Guiana may opportunistically feed during the nesting season. Similar hypotheses based on body mass change (St. Croix, US Virgin Islands; Eckert et al. 1989), mouth-opening patterns (Grenada, West Indies; Myers and Hays 2006), or gut temperature records (St. Croix, US Virgin Islands; Southwood et al. 2005; Casey et al. 2010) have been proposed for other leatherback nesting populations in the Atlantic Ocean. However, these hypotheses are based on inference without any information on the actual physiological status of the study individuals. Here we aimed to test whether leatherback turtles feed during the nesting season in French Guiana using the longitudinal monitoring of morphometric (body length, width, and mass) and physiological (glucose, TG, urea, calcium, and hematocrit) parameters as indicators of body condition and nutritional status in 35 leatherback females throughout their nesting season.

Material and Methods

This project respected the legal requirements of the country in which the work was performed and followed all institutional guidelines. This study was performed under Centre National de la Recherche Scientifique–Institut Pluridisciplinaire Hubert Curien (CNRS-IPHC) institutional license (B67-482-18 delivered by Departmental Direction of the Veterinary Services, Strasbourg, France, and the Police Prefecture of Bas Rhin) and under individual licences to J.-Y.G. (67-220 delivered by the Departmental Direction of the Veterinary Services, Strasbourg, France, and the Police Prefecture of Bas-Rhin).

Study Site

This study was conducted throughout the entire 2006 nesting season (March–July) at one of the world's largest nesting sites for leatherback turtles (Fossette et al. 2008*b*): Awala Yalimapo beach (5.7°N, 53.9°W), French Guiana, South America. Monitoring programs on this beach have been running since the late 1970s for individual identification, using first external metal tags (Monel tags, National Band and Tags) and then, since 1995, internal passive integrated transponder (PIT) tags (Trovan Euroid; Fossette et al. 2008*b*). All individuals considered in our study were marked remigrants (i.e., females tagged as nesters during previous seasons; Fossette et al. 2008*b*).

Field Protocol

Between March 15 and July 21, 2006, a 4-km-long stretch of the beach where most nesting events historically occur (Fossette et al. 2008*b*) was patrolled every night from 6:00 p.m. to 7:00 a.m. All remigrant turtles encountered during these patrols were individually identified by their PIT tag. Our monitoring consisted of (i) recording identity, date of oviposition, and body morphometrics; (ii) counting yolked eggs, weighing the entire clutch at the first observed oviposition, and sampling three yolked eggs from each clutch to estimate clutch mass; (iii) sampling blood during oviposition; and (iv) weighing females after oviposition, when they were returning to the sea (details are given below). This sequence of manipulations ensured minimal disturbance, as confirmed by direct observations of all manipulated turtles completing their oviposition and returning to lay subsequent clutches. In total, 35 females were monitored with complete measurements and blood samples for almost all successive clutches during their entire nesting season.

The longitudinal monitoring was performed as follows: (i) During each observed nesting event, morphometric measurements (standard curvilinear carapace length [SCCL] and standard curvilinear carapace width [SCCW]) were taken using a flexible measuring tape (± 0.5 cm, following Georges and Fossette 2006). (ii) At the first observed clutch of each turtle, before the first egg was laid, a fabric bag with its base closed by a knotted lace was fitted in the nest chamber. During oviposition, all eggs were collected in this fabric bag, and yolked eggs were simultaneously counted using a hand tally counter. Three yolked eggs were collected by hand during egg counting. Once the last egg was laid and before the female started covering its nest, the bag was removed from the nest. A bucket was inserted in the nest chamber, and the female's hind flippers were held by hand out of reach of the sand to prevent the nest chamber from being filled with sand during the clutch weighing. Meanwhile, the clutch was weighed in the bag (± 0.05 kg) using a handheld spring scale. After clutch weighing (~20 s), the bucket was removed, and the bag was replaced into the nest chamber. The lace was untied to open the bottom of the bag, which was then gently removed from the nest chamber. The eggs were hence redesposited into the nest chamber in a similar order to the one in which they had been laid. The flippers were released, allowing the turtle to cover the nest. Because of the heavy logistical needs of this protocol, only the first observed clutch of each turtle was weighed in this way. The mass of subsequent clutches was estimated by calculating the mean mass of the three yolked eggs collected during egg counting (± 0.1 g), then multiplying this value by clutch size. This estimation method for individual clutch mass was validated for the first observed clutches, because no significant differences were found between clutch mass weighed with the bag and clutch mass estimated from the three collected eggs (7.0 ± 0.3 kg vs. 6.7 ± 0.3 kg, respectively; paired *t*-test, $P = 0.48$, $t = -0.70$, $n = 33$ clutches). (iii) During each observed oviposition, a 6-mL blood sample was collected from the femoral rete system using a syringe. The blood was immediately transferred into heparinized polypropylene microtubes and placed in a refrigerated cool box until the patrol was finished. Hematocrit measurement was then performed (maximum 4 h after sampling) using one capillary tube of whole blood, and blood samples were centrifuged to separate plasma and blood cells. Samples were frozen (-20°C) until they could be analyzed at the IPHC, Strasbourg, France. (iv) After oviposition, turtles were weighed (± 0.2 kg) when returning to the sea using a customized harness and an electronic spring scale fixed to a 4.5-m-high carbon-fiber tripod equipped with a hoist (see details in Georges and Fossette 2006).

Reproductive Effort

For each individual, we defined the observed nesting period as the period between the first and last observed clutches. Despite our exhaustive night patrols, some clutches were not observed, because leatherbacks may nest outside the hours of our patrol schedule. Therefore, we calculated the estimated clutch frequency (ECF) for each female following Frazer and Richardson (1985). The ECF is the total number of clutches that a turtle is believed to have deposited during its nesting season, taking into account the intermediate nonobserved clutches (based on the mean internesting duration of 10 d in leatherbacks; Girondot and Fretey 1996). This also permitted the calculation of cumulative clutch size and cumulative clutch mass for each female by multiplying its ECF by the mean clutch size and by the mean clutch mass of its observed clutches, respectively. We also defined the level of reproductive effort (LRE), adapted from Hamann et al. (2002), as an index of the progress of the season. For a given clutch (x), LRE was calculated as $\mathrm{LRE}_{\text{at clutch } x} = (x/\mathrm{ECF}) \times 100$. LRE provides a better proxy of the relative reproductive effort through time compared with clutch rank. For instance, for one turtle laying 5 clutches (ECF = 5) and a second turtle laying 10 clutches (ECF = 10), LRE for a given clutch (e.g., the fourth clutch) will be twice as high for the turtle with the lowest ECF (LRE = 80%) in comparison with the turtle with highest ECF (LRE = 40%).

Maternal Body Condition Index (BCI)

Maternal BCI was calculated for each individual at every observed clutch as an indicator of individual health (Peig and Green 2009). Because variation in body mass can be associated with differences in nutritional status as well as structural size, differences between body mass and structural size thus constitute a good index of nutritional state (Schulte-Hostedde et al. 2005). BCI was calculated following Saraux et al. (2011). First, a structural size index (SSI) was calculated using body length and body width, both of which are good descriptors of sea turtle structural size (Georges and Fossette 2006). Because SCCL and SCCW were correlated (linear regression, $P < 0.001$, $R^2 = 0.41$), we used a principal component analysis to establish the SSI. The first principal component between these two parameters explained 82% of the variation. Second, the

body condition was defined as the residuals of a regression of body mass on SSI (Schulte-Hostedde et al. 2005; Saraux et al. 2011). Because maternal BCI was calculated for each individual at every observed clutch throughout the observed nesting period, we used a linear mixed-effect (LME) model with the identity of the turtle as a random factor.

Plasma Parameter Concentrations

Plasma metabolites (glucose, TG, and uric acid or urea) are associated with specific metabolic pathways involved in the mobilization of successive body reserves (Robin et al. 1998) and are commonly used as indicators of the physiological and nutritional status in animals. In turtles, urea is described as the main product of protein catabolism instead of the uric acid reported in birds (Dessauer 1970; Bonnet 1979). Furthermore, the fact that, in sea turtles, urea does not play the osmoregulatory role reported in other marine vertebrates (Lutz 1997; Acher et al. 1999) gives assurance that plasma urea concentrations are not biased by any physiological processes other than protein metabolism. Urea was thus used as an indicator of protein catabolism.

Plasma concentrations of metabolites were measured using 10 μL of undiluted plasma with commercial enzymatic colorimetric kits (glucose: Glucose-RTU, 61 269/61 270; TG: TG-PAP 150, 61 236; urea: Urea-Kit S180, 61 912/61 913; bioMérieux). Because calcium may be associated with egg production, plasma concentrations of calcium were also measured using 6 μL of undiluted plasma with commercial colorimetric method kits (Ca-Kit 61041, Thermo Ficher Scientific).

Statistical Analyses

Results are given as means ± standard error (range). Statistical tests were processed with R software (2.10.1). Normality was checked before each test using the Shapiro-Wilk test. Tests for correlation were run with linear regression or the Spearman correlation test. Changes in morphometric measurements, body condition, physiological parameters, and clutch mass throughout the observed nesting period were investigated using LME when residuals fitted with normal distribution and generalized estimating equation (GEE) model when residuals did not fit with normal distribution. This allows controlling for pseudoreplication by including individual identity as a random factor. Multiple comparisons were then applied with a Tukey's post hoc test (after LME) or Wilcoxon paired test (after GEE). Potential changes in reproductive output, body mass, body condition, and physiological parameters throughout the observed nesting period were investigated, considering LRE to be the timescale.

Results

Morphometrics and Blood Values at First Observed Clutch

At the first observed clutch, the 35 nesting females were a mean of 159.0 ± 1.5 cm long (SCCL; range, 141.5–172.0 cm) and 116.0 ± 1.0 cm wide (SCCW; range, 107.5–125.0 cm) and weighed 409.0 ± 8.9 kg (range, 289.6–508.0 kg), corresponding to a mean maternal BCI of 25.1 ± 1.8 (range, 4.7–45.3). At that time, mean physiological parameter values for the 35 females were as follows: hematocrit, 40.5% ± 1.0% (range, 26.1%–57.0%); glucose, 12.46 ± 0.64 mmol/L (range, 8.66–24.00 mmol/L); TG, 12.89 ± 0.56 mmol/L (range, 2.10–19.60 mmol/L); urea, 1.14 ± 0.08 mmol/L (range, 0.33–2.13 mmol/L); calcium, 3.25 ± 0.18 mmol/L (range, 1.40–5.81 mmol/L).

At the first observed clutch, there were no significant relationships between maternal BCI and plasma concentrations of glucose, TG, and urea ($P = 0.32$, 0.48, and 0.23, respectively). We did, however, find a positive trend between maternal BCI and calcium ($P = 0.067$, $R^2 = 0.10$) and a significant positive relationship between maternal BCI and hematocrit ($P = 0.01$, $R^2 = 0.18$). Statistical significances were similar when maternal body mass was considered instead of BCI.

Reproductive Parameters, Morphometrics, and Blood Values

The observed nesting period of the 35 study individuals (i.e., the time elapsed between the first and the last observed clutches) lasted, on average, 71.2 ± 2.6 d (range, 40–98 d; $n = 35$), with a mean internesting interval of 9.9 ± 0.1 d (range, 8.7–11.1 d; $n = 35$; individual means). Individual ECF averaged 8.3 ± 0.3 clutches per season (range, 5–12 clutches

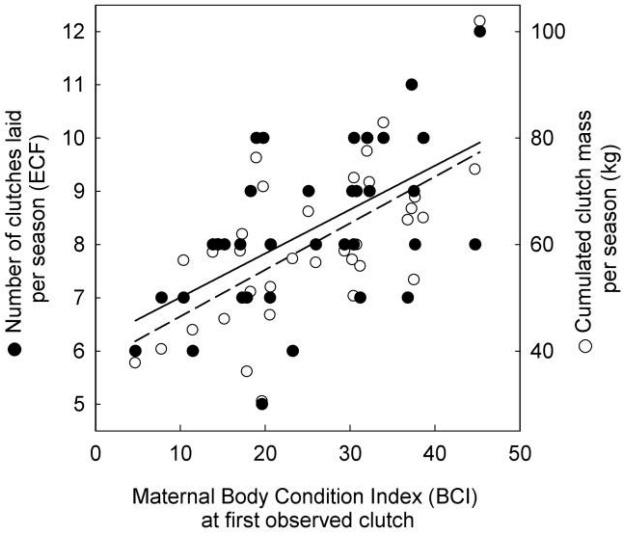

Figure 1. Relationships between maternal body condition index at first observed clutch and reproductive output indices: number of clutches laid per season (filled circles, solid line) and cumulative mass clutches per season (open circles, dotted line).

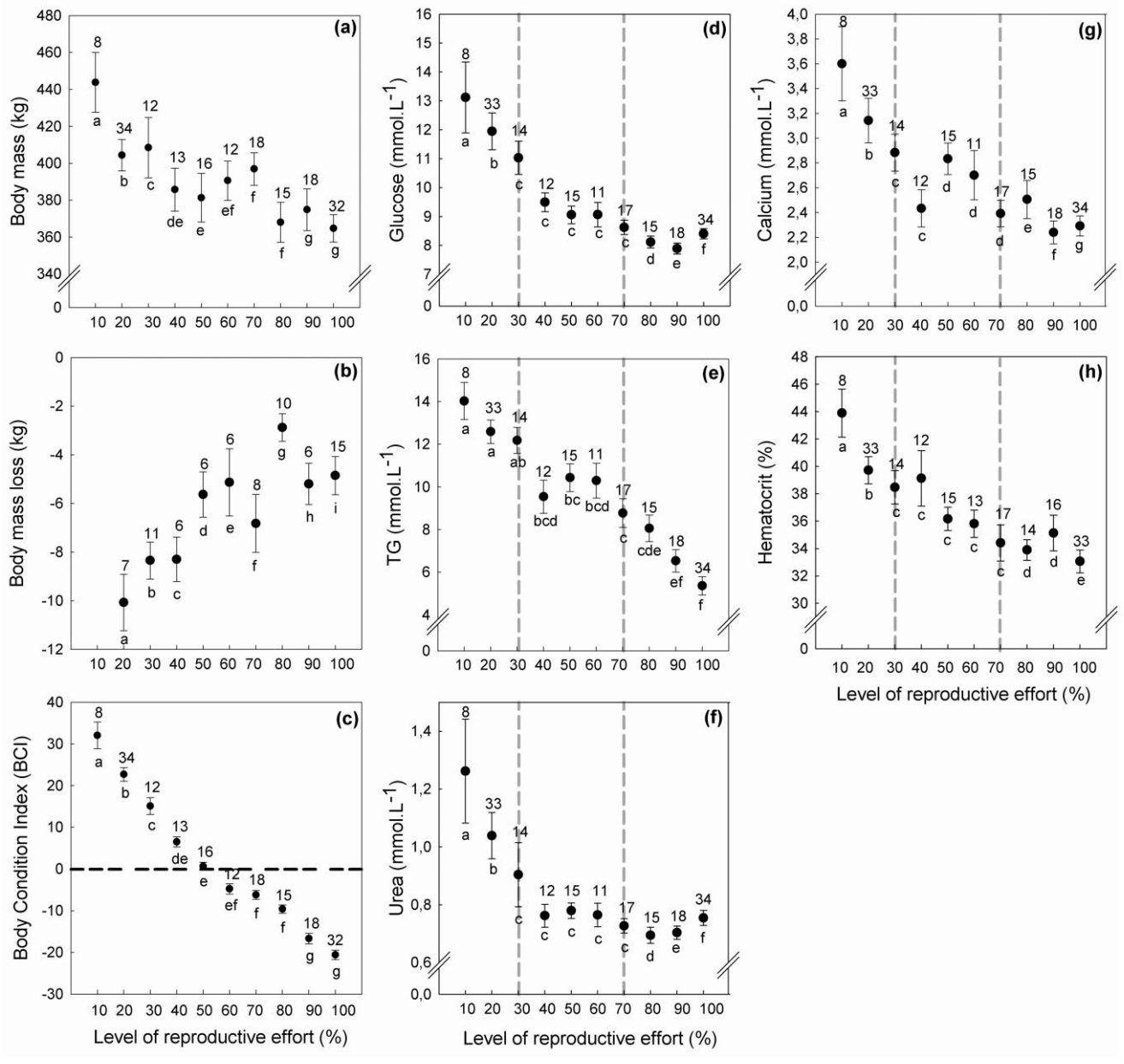

Figure 2. Changes in maternal morphometric (*a–c*) and physiological (*d–h*) values throughout the nesting period (represented by the level of reproductive effort [LRE]). Values are means ± standard error. Letters refer to significant differences ($P < 0.05$), numbers refer to the number of individuals represented in each LRE class, and vertical dashed gray lines refer to 30% and 70% LRE, where major physiological patterns occurred (see "Results"). TG = triacylglyceride.

per season; $n = 35$) and was positively related to the duration of the observed nesting period ($P < 0.001$, $R^2 = 0.91$, $n = 35$). Over the entire nesting period, the mean clutch size was 86.9 ± 2.2 eggs per clutch (range, 44–112 eggs; $n = 35$) for a mean clutch mass of 7.2 ± 0.2 kg (range, 2.6–10.3 kg; $n = 35$). During the entire nesting period, the cumulative clutch size and cumulative clutch mass averaged 717 ± 28 eggs (range, 305–1,129 eggs; $n = 35$) and 59.7 ± 2.4 kg (range, 30.6–102.2 kg; $n = 35$), respectively.

The duration of the observed nesting period and the ECF were positively related to maternal morphometrics (SCCL $P = 0.02$, $R^2 = 0.15$ in both cases; maternal body mass at the first observed clutch: $P = 0.019$, $R^2 = 0.15$, and $P = 0.01$, $R^2 = 0.18$, respectively; maternal BCI at first observed clutch: $P < 0.001$, $R^2 = 0.31$, and $P < 0.001$, $R^2 = 0.66$, respectively; fig. 1). The cumulative clutch size was positively related to maternal body mass and BCI at the first observed clutch ($P = 0.01$, $R^2 = 0.18$, and $P < 0.001$, $R^2 = 0.34$, respectively) and tended to be positively related to SCCL ($P = 0.062$, $R^2 = 0.10$). The cumulative clutch mass was positively related to maternal body

Table 1: Morphometric and physiological values of the 35 leatherback females monitored throughout the nesting period

LRE (%), by morphometric or plasma value	Mean	SE	Range	*n*
Morphometrics:				
Body mass (kg):				
0–10	443.8	16.2	382.6, 496.6	8
11–20	404.4	8.5	289.6, 508.0	34
21–30	408.5	16.4	286.2, 481.4	12
31–40	385.7	11.6	337.2, 467.2	13
41–50	381.3	13.2	281.0, 464.0	16
51–60	390.6	10.6	339.4, 447.0	12
61–70	396.9	8.8	340.0, 463.2	18
71–80	368.0	10.8	272.0, 429.6	15
81–90	374.8	11.3	299.0, 450.8	18
91–100	364.7	7.4	264.6, 440.0	32
Body mass loss (kg):				
0–10				0
11–20	−10.1	1.2	−15.4, −5.4	7
21–30	−8.3	.8	−11.6, −3.4	11
31–40	−8.3	.9	−11.6, −5.0	6
41–50	−5.6	.9	−9.6, −3.8	6
51–60	−5.1	1.4	−11.2, −2.0	6
61–70	−6.8	1.2	−11.6, −2.0	8
71–80	−2.9	.7	−5.6, −1.0	10
81–90	−5.2	.8	−8.0, −2.8	6
91–100	−4.8	.8	−10.8, −.6	15
Body condition index:				
0–10	32.0	3.2	18.9, 45.3	8
11–20	22.7	1.6	4.7, 44.7	34
21–30	15.1	2.0	5.7, 28.0	12
31–40	6.5	1.2	.1, 15.9	13
41–50	.7	.9	−6.9, 8.2	16
51–60	−4.8	1.2	−13.1, .0	12
61–70	−6.2	1.0	−13.5, .1	18
71–80	−9.6	1.0	−15.1, −3.6	15
81–90	−16.7	1.3	−29.1, −8.5	18
91–100	−20.6	1.1	−35.3, −5.8	32
Plasma values:				
Glucose (mmol/L):				
0–10	13.12	1.22	9.68, 16.88	8
11–20	11.95	.63	8.66, 24.05	33
21–30	11.03	.60	9.06, 17.27	14
31–40	9.50	.33	7.16, 11.15	12
41–50	9.06	.30	7.27, 10.96	15
51–60	9.06	.42	7.62, 12.40	11
61–70	8.62	.25	6.38, 10.66	17
71–80	8.11	.20	7.23, 10.46	15
81–90	7.89	.19	6.81, 9.72	18
91–100	8.40	.17	6.41, 10.70	34
Triacylglycerides (mmol/L):				
0–10	14.02	.90	10.97, 18.03	8
11–20	12.59	.56	5.06, 19.59	33
21–30	12.18	.61	8.15, 16.15	14
31–40	9.54	.77	3.04, 13.26	12
41–50	10.43	.65	7.21, 15.36	15

Table 1 (*Continued*)

LRE (%), by morphometric or plasma value	Mean	SE	Range	*n*
51–60	10.29	.82	7.46, 16.74	11
61–70	8.77	.68	4.70, 14.99	17
71–80	8.06	.62	4.75, 11.41	15
81–90	6.53	.53	3.42, 11.90	18
91–100	5.36	.43	1.56, 11.89	34
Urea (mmol/L):				
0–10	1.26	.18	.44, 2.12	8
11–20	1.04	.08	.33, 2.13	33
21–30	.90	.11	.53, 2.02	14
31–40	.76	.04	.60, 1.13	12
41–50	.78	.03	.56, .97	15
51–60	.76	.04	.57, .97	11
61–70	.73	.02	.60, 1.02	17
71–80	.69	.03	.44, .93	15
81–90	.70	.02	.63, .98	18
91–100	.75	.03	.53, 1.25	34
Hematocrit (%):				
0–10	43.9	1.7	35.0, 50.6	8
11–20	39.7	1.0	26.1, 57.0	33
21–30	38.5	1.2	30.5, 48.4	14
31–40	39.1	2.0	29.0, 53.5	12
41–50	36.2	.8	31.5, 42.0	15
51–60	35.8	1.0	30.0, 44.0	11
61–70	34.4	1.3	30.0, 52.0	17
71–80	33.9	.7	30.0, 38.0	15
81–90	35.1	1.3	28.0, 49.5	18
91–100	33.1	.8	26.0, 48.5	33
Calcium (mmol/L):				
0–10	3.60	.30	2.71, 5.15	8
11–20	3.14	.18	1.40, 5.81	33
21–30	2.88	.15	2.38, 4.46	14
31–40	2.43	.15	1.22, 3.10	12
41–50	2.83	.13	2.25, 3.79	15
51–60	2.70	.20	1.61, 4.18	11
61–70	2.40	.11	1.49, 3.52	17
71–80	2.50	.15	1.98, 4.26	15
81–90	2.24	.09	1.50, 3.36	18
91–100	2.29	.08	1.39, 3.35	34

Note. The timescale considered in this study is the level of reproductive effort (LRE; see "Material and Methods"). SE, standard error.

mass and BCI at the first observed clutch ($P = 0.001$, $R^2 = 0.27$, and $P < 0.001$, $R^2 = 0.41$, respectively; fig. 1) and also to SCCL ($P = 0.029$, $R^2 = 0.13$).

The duration of the observed nesting period was positively related to initial plasma concentrations of urea ($P = 0.037$, $R^2 = 0.12$) and calcium ($P = 0.031$, $\rho = 0.36$). ECF tended to be positively related to initial plasma concentrations of urea ($P = 0.057$, $R^2 = 0.10$) and was positively related to calcium ($P = 0.028$, $\rho = 0.37$). The duration of the observed nesting period and the ECF were not related to initial hematocrit or plasma concentrations of TG and glucose ($P > 0.13$ in all cases).

Changes in Morphometric Values throughout the Nesting Period

A significant but nonlinear decrease in maternal body mass was observed throughout the observed nesting period (LME, $P < 0.001$; fig. 2*a*; table 1). Maternal mass loss was high during the first internesting interval (10 kg) and decreased rapidly during the first 50% of LRE before stabilizing at approximately 5 kg between two consecutive clutches thereafter (Wilcoxon tests between successive LRE classes, $P < 0.01$ in all cases; fig. 2*b*; table 1). Maternal BCI decreased throughout the nesting period

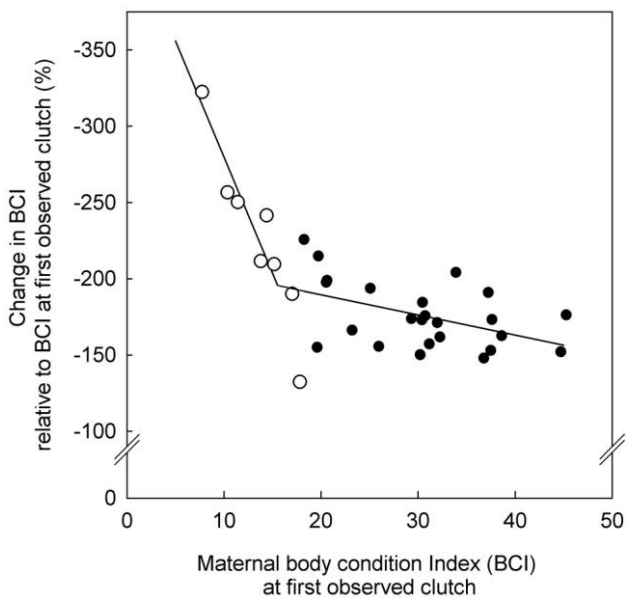

Figure 3. Change in maternal body condition index (BCI) over the nesting season. The piecewise regression (solid line) of maternal BCI change (BCI at the last observed clutch relative to BCI at the first observed clutch; piecewise regression, $P < 0.001$, $R^2 = 0.77$) revealed a break point, with a dramatic loss of BCI at the offset of the nesting season for females with an initial BCI <18.3 (open circles, regression slope −15.2) compared with other females (filled circles, regression slope −1.3).

(LME, $P < 0.0001$; fig. 2*c*; table 1), mostly linearly, although the highest rates were recorded during the first half of the nesting period (Tukey's post hoc, $P < 0.01$ in all cases).

For the 32 females weighed at their last observed clutch, maternal body mass at the last observed clutch was 364.7 ± 7.4 kg (range, 264.6–440.0 kg), corresponding to a mean total body mass loss of 46.8 ± 2.6 kg (range, 23.6–79.8 kg), or 0.7 ± 0.0 kg/d (range, 0.4–1.0 kg/d). There was a positive relationship between total maternal body mass loss and maternal body mass at the first observed clutch ($P = 0.003$, $R^2 = 0.54$; $n = 32$ females). Maternal BCI at the last observed clutch was −20.6 ± 1.1 (range, −35.23 to 5.8), corresponding to a BCI change of −188.4% ± 6.6% (−322.3 to −132.3) relative to maternal BCI at the first observed clutch. A piecewise regression of maternal BCI change relative to maternal BCI at the first clutch ($P < 0.001$, $R^2 = 0.77$; fig. 3) revealed a break point at an initial BCI of 18.3, and the BCI loss for the 8 females with an initial BCI <18.3 was 10-fold higher than for other females (fig. 3). SCCL and SCCW of these 8 individuals did not differ from that of the other females (*t*-test, $P > 0.2$ in both cases), yet they were lighter at the first clutch (364.1 kg vs. 427.3 kg; *t*-test, $P = 0.005$, $t = -3.43$).

Maternal BCI at the last observed clutch was negatively related to the duration of the observed nesting period and to ECF ($P < 0.001$, $R^2 = 0.47$, and $P < 0.01$, $R^2 = 0.58$, respectively). However, the change of maternal BCI relative to initial BCI was not related to the duration of the observed nesting period or to ECF ($P > 0.28$ in both cases).

Changes in Blood Values throughout the Nesting Period

Similarly to morphometric values, hematocrit, glucose, urea, and calcium values decreased throughout the nesting period (GEE, $P < 0.0001$, $\chi^2_{\text{Wald}} = 67.7$; GEE, $P < 0.0001$, $\chi^2_{\text{Wald}} = 97.2$; GEE, $P < 0.0001$, $\chi^2_{\text{Wald}} = 35.4$; and GEE, $P < 0.0001$, $\chi^2_{\text{Wald}} = 60.2$, respectively), and particularly during the first 30% LRE (Wilcoxon paired tests, $P < 0.03$ in each case; fig. 2*d*, 2*f*–2*h*). Thereafter, these parameters did not vary significantly until 70% LRE (Wilcoxon paired tests, $P > 0.06$ in each case), and a slight but significant increase in plasma glucose, urea, and calcium occurred at the very end of the nesting season (Wilcoxon paired tests, $P < 0.03$ in each case; fig. 2*d*, 2*f*–2*h*). Plasma TG decreased throughout the nesting period (LME, $P < 0.0001$; fig. 2*e*; table 1). The decrease was not significant during the first 30% LRE (Tukey post hoc test, $P > 0.037$) and then became significant until the end of the nesting period (Tukey post hoc tests, $P < 0.001$ in all cases).

Changes in plasma glucose, urea, and calcium (measured at the last clutch relative to the first clutch) were not related to the duration of the observed nesting period or to ECF ($P > 0.07$ in all cases). Interestingly, changes in hematocrit and TG levels were positively related to the duration of the observed nesting period and to ECF (hematocrit: $P < 0.001$, $R^2 = 0.30$, and $P < 0.001$, $R^2 = 0.31$, respectively; TG: $P = 0.033$, $R^2 = 0.11$, and $P = 0.06$, $R^2 = 0.10$, respectively).

Changes in Reproductive Output throughout the Nesting Period

Clutch size and clutch mass did not vary throughout the nesting period (LME, $P > 0.14$ and $P = 0.059$, respectively; table 2). Likewise, no changes were observed in mean egg mass over the nesting period (LME, $P = 0.42$).

Discussion

This study aimed to determine whether leatherbacks nesting in French Guiana are capital breeders by assessing whether they experience anorexia during reproduction. We monitored individual body morphometrics and plasma concentrations of metabolites, calcium, and hematocrit in 35 gravid females throughout their nesting season.

Morphological Evidence of Fasting in Nesting Leatherback Turtles

At the onset of their nesting season, leatherbacks nesting in French Guiana weighed, on average, 410 kg, with a high interindividual variability, because the heaviest individuals (510 kg) were almost twice as heavy as the smallest ones (290 kg). Our results confirm that leatherbacks in French Guiana are heavier and larger than those in other nesting populations (Georges and Fossette 2006).

Table 2: Reproductive output of the 35 leatherback females monitored throughout the nesting period

LRE (%), by clutch size and mass	Mean	SE	Range	*n*
Clutch size (no. eggs/clutch):				
0–10	87.5	10.3	33.0, 130.0	8
11–20	87.9	3.9	37.0, 131,0	32
21–30	89.8	5.0	59.0, 117.0	13
31–40	88.6	3.7	67.0, 113.0	12
41–50	92.0	3.9	61.0, 114.0	16
51–60	91.5	4.2	59.0, 115.0	13
61–70	91.8	2.6	77.0, 112.0	16
Clutch mass (kg):				
0–10	6.6	.7	2.6, 8.6	8
11–20	7.0	.3	2.7, 10.3	32
21–30	7.7	.4	5.3, 9.8	13
31–40	7.6	.3	5.7, 9.2	12
41–50	7.6	.4	4.7, 10.1	15
51–60	7.7	.4	5.4, 9.9	10
61–70	7.8	.3	6.5, 9.3	12

Note. The timescale considered in this study is the level of reproductive effort (LRE; see "Material and Methods"). SE, standard error.

In this study, the duration of the nesting period averaged 71 d, during which leatherbacks nested every 10 d, laying a total of 8 clutches of 87 eggs each (i.e., 60 kg of eggs in total). These phenology values are consistent with those previously reported in French Guiana (Girondot and Fretey 1996) and illustrate the extent of reproductive output in this species.

Our longitudinal monitoring shows that the reproductive output was related to maternal morphometrics, with females that were longer, heavier, and in better condition reproducing over a longer nesting season, laying more clutches, and producing more eggs. In Pacific Costa Rica, larger leatherbacks have been reported to produce larger clutches (Price et al. 2004), despite contradicting results involving this population (Reina et al. 2002; Wallace et al. 2007). Similar positive relationships between maternal size and clutch size have also been reported, not only in green and loggerhead turtles (Broderick et al. 2003) but also in other reptiles (reviewed in Shine 2005). In reptiles, such relationships are associated with physical constraints of body size but also energy stores (Olsson and Shine 1997). The fact that leatherbacks in French Guiana produce larger and more numerous clutches than other populations (e.g., Pacific Costa Rica: Reina et al. 2002; Price et al. 2004; Wallace et al. 2007; Equatorial Guinea: Honarvar et al. 2011) is thus likely to be related to their larger body size and may also be related to their better body condition.

During their 71-d nesting period, leatherbacks lost, on average, 47 kg of body mass, corresponding to ~11% of their body mass at the first clutch. This rate of mass loss (i.e., 0.7 kg/d) is higher than in the green turtle (mean ± SD, 0.22 ± 0.15 kg/d [$n = 14$] for 166-kg females [i.e., 5% of initial body mass]; calculated from Hays et al. 2002) and the hawksbill turtle (0.112 ± 0.1 kg/d [$n = 75$] for 80-kg females [i.e., 7% of initial body mass]; Santos et al. 2010) and may result from size-specific differences. The rate of maternal body mass loss decreased nonlinearly throughout the nesting season, lowering by ~50% during the first 2–4 wk before remaining relatively low and stable throughout the rest of the season. This decrease in maternal body mass suggests that leatherbacks nesting in French Guiana do not feed during the internesting intervals or that feeding may not be sufficient to maintain body mass throughout reproduction. To date, such patterns in body mass change have not been reported in any other sea turtles, probably because previous longitudinal monitoring was not sufficiently extensive (Eckert et al. 1989; Hays et al. 2002). Interestingly, clutch mass did not change as the season proceeded, as reported in Pacific leatherbacks (Wallace et al. 2007). This contrasts, however, with leatherbacks in Equatorial Guinea, where clutch mass decreased through time (Honarvar et al. 2011). Considering maternal body mass loss results from maternal maintenance and egg production, our results suggest that leatherbacks decrease their maintenance throughout the nesting season. Additional studies are required to estimate how much maternal maintenance and egg production contribute to maternal mass loss and to assess physiological and/or behavioral cues involved in the observed patterns.

The body mass lost by leatherbacks was lower than clutch mass, not only when considering any given clutch but also when considering cumulative values over the entire season. The observed discrepancy in mass budget may result from water ingestion during the internesting intervals to supplement maternal body water for egg development. However, routes for water loss toward reproduction have not been addressed in the leatherback. Water ingestion may occur by drinking but also by feeding on water-rich jellyfish, as suggested by Southwood et al. (2005). Interestingly, our results show that hematocrit decreased throughout the season. Decreasing hematrocrit is com-

monly associated with anaemia (i.e., a decrease in health status; Tavares-Dias et al. 2009) and is consistent with the decrease in maternal body condition observed throughout the study season. The observation of a decrease in body condition as the season proceeds suggests that feeding does not occur and that water ingestion is most likely to happen by drinking. Consistently, drinking behavior has been previously suggested in leatherbacks nesting in French Guiana (Fossette et al. 2008*a*). We further tested whether jellyfish are actually ingested by assessing plasma metabolite levels throughout the nesting season via a complementary longitudinal monitoring of physiological parameters.

Plasma-Based Evidence of Fasting in Nesting Leatherback Turtles

Concurrently with the decrease in morphometric values, significant decreases in plasma concentrations of glucose, TG, and urea over the nesting period corresponded to three phases. During the first 30% of the nesting season, plasma glucose and urea decreased concurrently with steady high levels of TG. During most of the remaining nesting season, plasma glucose and urea levels remained low and steady, whereas TG levels decreased linearly through time until the very end of the season, when glucose and urea levels increased slightly yet significantly. Those profiles of plasma metabolites are similar to those reported in long-term fasting animals (Groscolas 1986; Cherel et al. 1988; Castellini and Rea 1992) and thus strongly suggest that leatherbacks are anorexic during the nesting season (Miller 1997).

At the onset of the season, leatherbacks nesting in French Guiana showed high levels of glucose compared with other leatherback nesting populations (Deem et al. 2006; Harms et al. 2007; Harris et al. 2011; Honarvar et al. 2011), suggesting possible feeding shortly before the first nesting event. After the first clutch, glucose levels decreased by 30%, as also reported in fasting green (32%) and Kemp's ridley (*Lepidochelys kempii*; 36%) turtles (Moon et al. 1999). As the season proceeds, plasma TG levels decreased dramatically by 50% from the first to the last clutch, as also reported in nesting green turtles (Hamann et al. 2002). In long-term fasting animals, such TG decline has been associated with the mobilization of fat stores (referred to as phase II of fasting; Cherel et al. 1988). In addition, the decrease in plasma TG over the nesting period was positively related to the duration of the nesting season and ECF, suggesting that leatherbacks rely chiefly on lipid reserves during reproduction. In sea turtles, body lipids may be stored in large quantities in visceral fat (Moon et al. 1999), the maternal yolk of atretic large follicles (Kuchling and Bradshaw 1993), and subcarapace fat (Kwan 1994), particularly in the leatherback (Davenport et al. 2011). Concurrently, the low and steady levels of plasma urea observed from the first third of the nesting season indicate that leatherbacks use a protein-sparing strategy similar to that observed in long-fasting birds and mammals (Cherel et al. 1988). This supports our conclusion that leatherbacks are anorexic during the nesting season in French Guiana, contradicting recent conclusions (Fossette et al. 2008*a*). A similar conclusion has been recently proposed in the hawksbill turtle by Goldberg et al. (2012), who reported high levels of leptin, the appetite-suppressing hormone, during the nesting season.

At the very end of the nesting period, urea increased slightly yet significantly. This may indicate a shift from lipid to protein catabolism, as reported during the transition toward the end of long-term fasting while lipid body stores are depleted and body proteins are mobilized (phase III; Cherel et al. 1988) and as suggested in green turtles (Hamann et al. 2002). Hormonal refeeding signals (via corticosterone) that lead animals to stop reproduction have been reported in sea birds (Groscolas et al. 2008; Spée et al. 2010). Similar hormonal signals may occur in sea turtles and are likely to be mediated by the hunger-stimulating ghrelin, as recently reported in nesting hawksbill turtles (Goldberg et al. 2012). Such hormonal pathways triggering the end of the reproduction should be investigated in leatherbacks.

Evidence of Morphological and Physiological Threshold in Nesting Leatherback Turtles

When considering a maternal BCI based on morphological metrics (SCCL, SCCW, and body mass), we showed that all leatherbacks began their reproduction with a positive BCI. Such BCI values have been formerly reported as indicative of the health of individual animals (Peig and Green 2009) and suggest that all leatherbacks had significant amounts of body reserves when entering in reproduction. Considering their reproductive strategy, we expect that females should have reached a minimum level of body condition necessary to induce reproduction, as previously reported in capital breeding snakes (Naulleau and Bonnet 1996) and suggested in sea turtles (Hays 2000). Interestingly, the body condition of females starting reproduction with BCI <18 deteriorated dramatically during reproduction compared with others (fig. 3). Furthermore, we showed that females in better condition do indeed lay more clutches during the season than other individuals. This indicates that the costs of reproduction have more deleterious effects on females with poorer body condition. Consistently, only a small proportion of study females (8 [25%] of 32 individuals) started reproduction with BCI values below this threshold. The wide range of levels of physiological parameters recorded at the first clutch makes it impossible to identify any particular threshold value for these parameters at the start of reproduction.

At the end of the nesting season, the interindividual variability in plasma concentrations was very low (fig. 2; table 1). This may characterize some minimum thresholds associated with the end of reproduction. For instance, BCI values became negative during the period where leatherbacks rely on lipid reserves, which suggests a possible threshold in BCI changes that is associated with the shift in metabolic paths. As far as metabolites are concerned, the shift from lipid to protein metabolism indicates that lipid stores may be a limiting factor for reproduction in leatherbacks. Similarly, the positive relationship that we found between plasma calcium and both maternal condition and reproductive output suggests that calcium is a critical

component of reproduction in leatherbacks. This may be related to the fact that leatherback's eggs are heavily calcified (~1.23 g calcium per egg; Bilinsky et al. 2001) and that their large cumulative clutch size may result in high calcium requirements throughout the entire season. The relevance of calcium in leatherback reproduction is further consistent with a recent study showing that hatching and emergence success are related to maternal calcium levels in this species (Perrault et al. 2012).

Drent and Daan (1980) emphasized the importance of body condition in reproduction and postulated that the amount of reserves at the onset of breeding (i.e., the "capital") acts on the amount of energy devoted to breeding. This is particularly true for capital breeders (Naulleau and Bonnet 1996). As a whole, our results provide evidence that leatherback females are anorexic during the nesting season and lead to the conclusion that they operate as capital breeders by relying on stored body reserves to ensure their reproduction without jeopardizing their own body condition while not feeding during reproduction. Similar combined approaches should be implemented at other sites where sea turtles have been suggested to feed during the nesting season to provide a better understanding of reproductive strategies in these species.

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