Respiratory Physiology of Adult Leatherback Turtles (Dermochelys coriacea) While Nesting on Land

FRANK V. PALADINO¹, JAMES R. SPOTILA², MICHAEL P. O'CONNOR², AND ROBERT E. GATTEN, JR.³

¹Department of Biology, Indiana-Purdue University, Fort Wayne, Indiana 46805-1499 USA; [Fax: 219-481-6087; E-mail: Paladino@smtplink.ipfw.indiana.edu] ²Department of Bioscience and Biotechnology, Drexel University, Philadelphia, Pennsylvania 19104 USA; ³Department of Biology, University of North Carolina, Greensboro, North Carolina 27412 USA

ABSTRACT. – Leatherback turtles, *Dermochelys coriacea*, had a respiratory tidal volume (V_T) 11.3 times greater than predicted values for large, generalized reptiles, respiratory rate (f) 18% of predicted, minute lung ventilation ($V_{\rm F}$) 1.6 times greater than predicted, total lung volume (TLV) 1.25 times greater than predicted, and VT 29% of TLV. The generalized reptile has a VT that is only 3% of TLV. These leatherback data are similar to respiratory data for deep diving marine mammals that also have greater a V_T and V_E than their non-diving relatives. Mean oxygen consumption (\dot{V}_{α}) was 1.20 ml/kg/min (0.40 W/kg) while resting restrained in a net, 0.87 ml/kg/min (0.33 W/kg) while laying eggs, and 2.87 ml/kg/min (1.12 W/kg) while actively covering the nest. Resting respiratory quotient (RQ) was 0.69, indicating that these animals were probably fasting and burning fat. Core body temperature was 31.6°C and averaged 8–10°C above air temperature $(23.2\pm0.9^{\circ}C)$ and sand temperature (21.6 \pm 1.2°C), but only 2.5–5.1°C above surface water temperatures in the tropical Pacific Ocean. While active on land leatherbacks maintained a constant $V_{\rm E}/\dot{V}_{\rm O}$, ratio indicating that unlike green turtles (Chelonia mydas) they did not hyperventilate and experience respiratory alkalosis. During egg deposition leatherbacks exhibited a Lamaze pattern of shallow panting to compensate for increased respiratory stimulation and a slight respiratory alkalosis. For active green turtles plasma lactate was quite high and increased 11 times above resting values while for leatherbacks there was a modest trend toward increased plasma lactate but this never exceeded 2.5 times resting values and was quite low when compared to other active reptiles.

KEY WORDS. - Reptilia; Testudines; Dermochelyidae; Dermochelys coriacea; sea turtle; physiology; respiration; exercise; metabolism; oxygen consumption; thermoregulation; diving; allometry; Costa Rica

Leatherback turtles, Dermochelys coriacea, are among the deepest diving vertebrates (Eckert et al., 1986) and may have respiratory adaptations similar to other air breathing, diving vertebrates. These turtles are excellent subjects for studying the physical constraints that living under water has placed on the physiology of air breathing animals. Some respiratory adaptations seen in diving vertebrates include a larger than normal tidal volume (V_T), insensitivity of respiratory control systems to higher CO₂ concentrations, a greater oxygen carrying capacity of blood and other tissues, a higher tolerance to hypoxia at both the tissue and organismal level, and a more rigid structure in the non-respiratory passageways of the lungs (Jackson, 1985). Leatherbacks have twice the blood oxygen carrying capacity of smaller, shallow-diving marine turtles (Cheloniidae) (Lutcavage et al., 1992), a right-shifted oxyhemoglobin dissociation curve, and exceptionally large myoglobin stores (Lutcavage et al., 1990). All of these circulatory and tissue adaptations provide a better and more rapid oxygen delivery system to active tissues, a large oxygen storage capacity, and rapid respiratory turnover when gas exchange is possible.

Data on the physiology of the smaller green sea turtle, *Chelonia mydas*, during forced dives indicate that it exhibits extreme bradycardia, lowered metabolic rates, and peripheral vasoconstriction under such conditions (Berkson, 1966).

However, unrestrained free-diving reptiles and mammals exhibit greatly reduced respiratory, circulatory, and metabolic diving responses (Weinheimer et al., 1982; Guppy et al., 1986) in comparison with animals forced to dive. Leatherbacks are among the largest animals in the ocean and, being carnivorous, occupy an upper trophic level in the energy flow pyramid. Their diet is composed almost entirely of pelagic, soft-bodied organisms, primarily enidarians and ctenophorans (Brongersma, 1969; Mortimer, 1982; den Hartog and van Nierop, 1984; Bjorndal, 1985). Free-swimming leatherbacks have considerable control over their deep body temperatures. Frair et al. (1972) and Mrosovsky and Pritchard (1971) reported that individuals can have body temperatures T_b exceeding water temperatures. Countercurrent vascular heat exchangers in the front and rear flippers aid in retaining body heat (Greer et al., 1973). Changes in blood flow, in addition to an insulating subepidermal fatty layer and large body size, provide a mechanism for maintaining core temperatures well above that of the environment. Our measurements of body temperature (Standora et al., 1984) and metabolic rates (Paladino et al., 1990) indicate that adult leatherback turtles employ a thermoregulatory strategy termed gigantothermy in which they have a bradymetabolic (low) metabolism, large body size, and can alter circulation to change effective insulation thickness and maintain high, constant body temperatures in cold waters. They have constantly elevated body temperatures that permit the advantages of homoiothermy, despite a more reptilian-like metabolic physiology.

Despite the uniqueness of this species, little is known about its whole animal respiratory physiology, ecology, behavior, or diving adaptations. Therefore, the objectives of this study were to measure respiratory parameters such as tidal volume (V_T), respiratory rate (f), and minute ventilatory volume (V_E , the amount of air moved through the respiratory system in one minute), for restrained but resting, active, and egg laying leatherback turtles. We also measured and quantified the oxygen consumption (\dot{V}_{O_2}), carbon dioxide production (\dot{V}_{CO_2}), plasma lactic acid concentration, core body temperature (T_b), and respiratory quotient (RQ) of these turtles for all three conditions. Finally we made allometric comparisons of respiratory and metabolic data from leatherbacks with data from other reptiles and other diving vertebrates.

MATERIALS AND METHODS

We studied 13 adult female leatherback turtles (D. coriacea) in 1990, 1991, and 1992, at their nesting beaches near Tortuguero (Limon Province, Costa Rica) and Playa Langosta (Guanacaste Province, Costa Rica). We fitted a respiratory mask over the head of each leatherback and collected a minimum of 10 breaths of expired gas in a 100 liter Douglas bag as we did in previous metabolic studies (Paladino et al., 1990). Collection bags were never more than 75% full and f, VT, and the O2 and CO2 concentration of the expired air were determined using standard procedures (Prange and Jackson, 1976; Jackson and Prange, 1979; Paladino and King, 1984; Paladino et al., 1990). Expired air was passed through a dry gas meter to measure volume. We dried subsamples of gas and analyzed them for O2 and CO2 concentration using an Applied Electrochemistry CD-3 carbon dioxide analyzer and a Beckman C-2 oxygen analyzer in the field laboratories. We calibrated gas meters and verified CO2 and O2 data using an 0.5 ml Scholander respiratory gas analyzer. We measured body weight of the turtles using a 500 kg Chatillon dial scale calibrated to ± 5 kg using a tripod, cargo net, and winch to lift the turtle. We collected blood samples from the cervical sinus by the extraction method of Owens and Ruiz (1980) using a sterile 16 gauge needle and 50 ml syringe and immediately placed the samples on ice, transported them to the field laboratories, and centrifuged them. We fixed portions of the plasma from each sample in perchloric acid and froze them in liquid nitrogen for later analysis using the methods of Gatten (1985a). Plasma lactic acid data for resting and active turtles from all three years are presented as the means of at least two plasma subsamples from at least two different turtles each year.

Experimental Protocol. — In general, leatherbacks came ashore and nested undisturbed. After a female covered her nest and began to crawl towards the ocean, we placed a cargo net on the sand in front of her path. When she was on the net, we quickly wrapped it around her and secured it with ropes. We then covered the head with a soft, dark cloth and set up a large aluminum tripod around and above her. Using a two-ton winch and scale we hoisted the cargo net containing the turtle completely off the ground and measured body weight. When the turtle was elevated off the sand it became quiescent. We then lowered the turtle until it was only slightly elevated (about 20-40 kg registering on the scale) and placed the respiratory mask on the head. The turtle rested undisturbed between gas collections. After resting measurements were obtained we released the turtle from the net and allowed it to crawl on the beach. We collected gas samples during and after 30 minutes of such exercise activity. Our exercise regimen also included trials where a turtle would pull a 100 kg weighted sled through the sand. In three cases we obtained respiratory gas samples while turtles were laving eggs by placing the mask on the female after she began dropping eggs to reduce the chance of disturbing the process (females enter a trance-like state while laying eggs). In a fourth case, the sampling activity disturbed the nesting process and we discontinued attempts to obtain additional samples.

Table 1. Physiological respiratory variables of leatherback (*Dermochelys coriacea*) and green (*Chelonia mydas*) turtles (± 1 Standard Error, SE). See text for definitions.

	n	Weight kg ¹	f breaths/min ²	V _T liters ²	V _E ml/kg/min	\dot{V}_{O_2} W/kg ² [ml/kg/min] ³	$V_{\rm E} \dot{V}_{\rm O_2}$ ml/min/ ml O ₂ STPD	V _{CO2} [ml/kg/min]	RQ	т _ь °С
Leatherbacks (this study)										
Resting (Restrained)	10	354 ± 5	2.2 ± 0.1	6.2 ± 0.4	31.6 ± 1.3	0.40 ± 0.02	31.3		0.69	31.6 ± 0.3
3500. O						$[1.20 \pm 0.1]$		[0.70]		
Laving Eggs	3	300 ± 5	3.9 ± 0.3	2.7 ± 0.9	34.6 ± 1.1	0.33 ± 0.40	39.7		0.72	30.8 ± 0.2
						$[0.87 \pm 0.1]$		[0.63]		
Actively Exercising	10	366 ± 5	5.0 ± 0.6	7.4 ± 1.2	94.1 ± 11.6	1.12 ± 0.10	32.8		0.70	31.4 ± 0.4
						$[2.87 \pm 0.1]$		[2.01]		
Green Turtles (Jackson, 198	5)									
Resting	15	128	0.6 ± 0.1	4.5 ± 0.5	17.5 ± 0.32	$[1.0 \pm 0.1]$	17.6	[0.56]	0.56	
Active		128	6.4 ± 1.6	3.0 ± 0.4	151.7 ± 43.3	$[4.5\pm1.7]$	38.6	[4.05]	0.90	

Mean mass of a minimum of 3 turtles \pm calibration of scale

Mean of at least 3 different turtles in 2 separate trials ± 1 SE

 5 Matched single samples of V $_E,$ \dot{V}_{O_2} and \dot{V}_{CO_2} for calculation of RQ and V $_E/\dot{V}_{O_2}$

Data Analysis. — We calculated metabolic rates using standard procedures described in Prange and Jackson (1976) and Jackson and Prange (1979). Respiratory CO2 production (\dot{V}_{CO2}) was computed from the product of expired volume and the difference between fractional concentrations of CO2 in inspired and expired air. Computation of Vo, was corrected for the calculated difference between inspired and expired volumes, based on change in fractional concentration of nitrogen, as well as difference in O2 concentration in inspired and expired air. All gas measurements were corrected to STPD (standard temperature and pressure for dry air) using standard methods (Depocas and Hart, 1957). We calculated RQ from matched subsamples of respiratory gases. We measured these respiratory parameters on adult females while they were laying eggs (n = 3), actively covering the nest (n = 12), crawling (n = 10), and while quietly resting restrained in the cargo net (n = 13). We calculated RQ, V_E , and the V_E/\dot{V}_{O_2} ratio using methods described in Jackson (1985). We calculated lung volumes from data in Lutcavage et al. (1992) and obtained green turtle respiratory values from Jackson (1985). Allometric relationships for respiratory variables of reptiles and mammals were obtained from Dejours (1981), Dubach (1981), Calder (1984), and Paladino et al. (1990). Equations used were as follows (where M = mass in kg and m = mass in g, T_{h} = body temperature, RMR = resting metabolic rate, TLV = total lung volume, V_T = tidal volume, V_E = minute volume, f = respiratory rate in breaths per minute):

RMR (for generalized reptiles, $T_b = 30^{\circ}$ C, in W/kg) = 0.378(M)⁻¹⁷ RMR (for green turtles only, $T_b = 30^{\circ}$ C, in W/kg) = 0.317(M)⁻¹⁷⁴ RMR (for generalized mammals, $T_b = 39^{\circ}$ C, in W/kg) = 3.35(M)⁻²⁵ TLV (for reptiles, in ml) = 1.237(m)^{.75} TLV^m (for mammals, in ml) = 0.035(m)^{1.06} V_T (for reptiles, in ml) = 0.020(m)^{.80} V_T^m (for mammals, in ml) = 0.0075(m)^{1.0} V_E (for reptiles, in ml/min/g) = 0.41(m)^{.76} V_E^m (for mammals, in ml/min/g) = 1.57(m)^{.75} f (for reptiles, in breaths/min) = 20.6(m)⁻⁰⁴ f (for mammals, in breaths/min) = 209(m)⁻²⁵

RESULTS

Resting restrained leatherbacks (n = 10) had a mean V_T of 6.2 liters, with an *f* of 2.2 breaths/min and V_E of 31.6 ml/ kg/min (Table 1). Mean \dot{V}_{O_2} for these resting turtles was 1.20 ml/kg/min (0.40 W/kg) and mean \dot{V}_{CO_2} was 0.70 ml/kg/min resulting in a RQ of 0.69. While laying eggs leatherbacks (n = 3) increased *f* to 3.9 breaths/min (1.77 times resting value), while V_T dropped to 2.7 liters (44% of resting value) such that V_E was 34.6 ml/kg/min and remained within 10% of the resting value. The \dot{V}_{O_2} dropped 14% from 1.20 to 0.87 ml/kg/min for laying turtles when compared to those at rest. The RQ was similar for all conditions (0.69 while resting, 0.72 while laying, and 0.70 while active), indicating that these turtles were probably using fat reserves as a metabolic energy source and that they were not relying on anaerobic

metabolism when tested. Active leatherbacks (n = 10) crawling on the beach and covering their nests by throwing sand with their flippers, increased f 2.27 times resting values to 5.0 breaths/min and V_T 1.2 times resting to 7.4 liters such that V_E increased threefold to 94.1 ml/kg/min. The \dot{V}_{O_2} increased 2.84 times to 2.87 ml/kg/min (1.12 W/kg) when compared to resting values. Despite the fact that while active the V_E increased threefold, the V_E/ \dot{V}_{O_2} ratio remained constant (Table 1).

Lactic acid levels for resting leatherbacks were low, 156.9 μ g/ml, and increased only 2.21 times resting levels after 90 minutes of nesting activity, including vigorous movement, digging of the nest chamber, and throwing of sand while covering the nest for more than 20 minutes (Table 2). After 30 minutes of vigorous exercise (crawling on the beach and while pulling the weighted sled containing 100 kg of sand) lactic acid levels were only 2.04 times resting levels.

Leatherbacks had constant high core body temperatures that averaged 30.8°C while laying eggs, 31.6°C while at rest, and 31.4°C after 30 minutes of exercise (Table 1). There was no significant change in body temperature during activity (Student's t test, $n = 10, p \le 0.01$). Mean air temperature was 23.2 ± 0.9 °C, mean sand temperature was 21.6 ± 1.2 °C and inshore water temperatures within 150 m of the beach ranged from 26.0 to 29.1°C.

Mean \dot{V}_{CO_2} was 0.70 ml/kg/min at rest, 0.63 ml/kg/min while egg laying and 2.01 ml/kg/min while active. These

Table 2. Plasma and total body lactic acid concentrations ($\mu g / ml$ of plasma)(mean, standard deviation, standard error, and sample size) in leatherback turtles, alligators, and lizards while at rest and during activity. Leatherback data pooled for 3 years (1990–92).

	Mean	S.D.	S.E.	n
Leatherback (Dermochelys corid	<i>ucea</i>), adult, j	olasma, me	an $T_{h} = 31$.4°C
At Rest	156.9	11.2	9.1	10
After Exercise	320.3	149.8	122.3	10
After Nesting	346.8	30.8	21.8	2
Alligator (Alligator mississippiensi.	s ¹), juvenile, pl	lasma, T _b =	30°C	
At Rest	94			
After 4 min Swimming	1155			
Lizard (Anolis carolinensis2), ad	ult, total bod	y, $T_{\rm b} = 20^{\circ}$	C	
Cold Acclimated at Rest	136	20		5
Cold Acclimated				
after 30 sec Activity	591	87		7
Warm Acclimated at Rest	110	12		8
Warm Acclimated				
after 30 sec Activity	852	21		9
Lizard (Sceloporus jarovi2), adu	lt, total body.	$T_b = 20^{\circ}C$		
Cold Acclimated at Rest	18	3		9
Cold Acclimated				
after 30 sec Activity	433	40		8
Warm Acclimated at Rest	169	23		7
Warm Acclimated				
TT WITH THE CHINERCO				

¹ Gatten et al., 1991

² Gatten et al., 1985a

	Mass	fass f f	f^{\dagger}	V_{T} liters	V_T^1 liters	TLV liters	TLV ¹ liters	V _E ml/kg/m	V _E ¹ ml/kg/m	V _{O2} W/kg	RMR ¹ W/kg	$^{T_{b}}{}^{\infty}C$
	kg	breat	hs/min									
Leatherback (Derr	nochelys coria	cea)										
Resting	354	2.2	12.4	6.2	0.6	21.9	17.5	31.6	19.1	0.40	0.140	31.6 ± 0.3
Nesting		3.9		2.7				34.6		0.33		30.8 ± 0.2
Active		5.0		7.4				94.1		1.12		31.4 ± 0.4
Green Turtle (Che	lonia mydas)											2711 - 211
Resting	128		0.6		4.5		n/a		17.5		0.136	
Active	128		6.5		3.0				151.7		01100	
Hypothetical Gree	n Turtle (used	only for me	etabolic cor	nparison)					12, 12, 20,			
Resting	354	0.000		1							0.117	
Generalized Terres	strial Mammal										01117	
Resting	354		4.9		3.2		24.9		128.0		0.996	
Resting	128		6.3		1.2		9.2		59.8		0.773	
Resting	128		6.3		1.2		9.2		59.8		0.773	

Table 3. Allometric comparison of leatherback and green turtle respiratory data to hypothetical green turtle and generalized mammal predictions. Measurements of green turtle resting were taken while turtle was inverted (Jackson, 1985).

¹ Allometric predictions from equations in text for reptiles from Dejours (1981); allometric equations for mammals from Dubach (1981), Calder (1984), and Paladino et al. (1990).

values for CO_2 production mirror those for O_2 consumption (1.00 ml/kg/min at rest, 0.87 ml/kg/min while egg laying, and 2.87 ml/kg/min active), resulting in a constant RQ of about 0.70 for all conditions.

DISCUSSION

Leatherback respiratory rate at rest is higher than that reported for green turtles (Prange and Jackson, 1976; Jackson and Prange, 1979; Jackson, 1985) (Table 1) but the green turtles were tested while placed on their back and their breathing was labored. While active, leatherbacks had a respiratory rate 22% lower than that of active green turtles, while their tidal volume V_T was more than twice that of greens. The ratio of ventilation to oxygen consumption (V_E / \dot{V}_{o_2}) remained stable between rest and exercise, indicating that leatherbacks did not hyperventilate, despite an almost threefold increase in the metabolic rate while active. Both V_T and f increased during activity which indicated that leatherbacks had mechanisms to control both of these factors. In green turtles, V_E/\dot{V}_{O_2} increased from 17.6 at rest to 38.6 during exercise, indicating hyperventilation was occurring (Jackson, 1985). Hyperventilation in green turtles during activity was confirmed by an alkalotic shift in the measured blood pH, in addition, RQ increased from 0.56 to 0.90. It is difficult to interpret these changes in the respiration of green turtles because resting values were obtained from animals restrained on their backs, where the weight of the internal viscera was pressing upon the lungs, and cannot be considered normal.

Leatherbacks change their respiratory pattern during egg laying. They reduced V_T to 44% of the resting values and increased *f* by 1.77 times (Table 1). The RQ while laying (0.72) was similar to resting and active values (0.69 and 0.70, respectively) but the V_E / \dot{V}_{0_2} ratio increased 1.27 times from 31.3 at rest to 39.7 while laying. Thus, there appeared to be some hyperventilation during laying. These females appeared to be panting, with shallow breathing, and were probably becoming slightly alkalotic. This respiratory pattern is typical of domestic and wild mammals during labor

and delivery (van Tienhoven, 1983) and is typical of Lamaze breathing recommended for humans to prevent hyperventilation and respiratory alkalosis during labor and delivery.

Pain is a powerful stimulant to the inspiratory control center and will increase respiration in most vertebrates (Guyton, 1986). The process of passing many small eggs (opposed to a large fetus in mammals) may possibly cause stimulation of pain receptors of the reproductive tract. In human females during labor and delivery, the pain associated with parturition causes a mismatching of ventilation and metabolism and may result in hyperventilation and respiratory alkalosis. The same mismatching could possibly occur in leatherbacks. The reduction of V_T by leatherbacks in this study during egg laying tended to reduce the alkalotic effect of hyperventilation possibly caused by the pain stimulus axis described above.

Leatherbacks appeared to remain aerobic while resting, nesting, and exercising on the beach because they had low levels of lactic acid in their blood (Table 2). When plasma lactate values for leatherbacks and whole body lactates for other resting and active reptiles are compared (Table 2), leatherback plasma levels are quite low (Gatten, 1985b; Gatten et al., 1991; Gleeson, 1991). When compared to green turtles that increased plasma lactate 11.3 times above resting levels when exercised (Prange and Jackson, 1976; Jackson and Prange, 1979; Jackson, 1985), the modest increases of 2.04 times the resting levels for leatherbacks after exercising and 2.21 times the resting levels after completion of nesting were quite modest. Lactic acid values for resting leatherbacks were similar to those from resting alligators, Alligator mississippiensis, and the small lizards Anolis carolinensis and Sceloporus jarovi. In active leatherbacks, lactic acid levels increased 2.0-2.2 times resting levels after 30-90 min of exercise, while lizards increased lactate 4.7-7.7 times resting levels after 30 sec of exercise and alligators increased lactate 12.3 times basal levels after 4 min of exercise.

Data for mammals (rats and dogs) indicate that the lactate produced anaerobically during exercise is later oxidized to CO_2 during recovery and is referred to as the oxygen debt. In amphibians and reptiles, lactate produced during exercise is used as a substrate for immediate muscle glycogen replenishment during recovery (Gleeson, 1991). Our studies suggest that leatherbacks do not rely heavily on anaerobic metabolism during activity on the beach and that the low levels of lactate that are produced are quickly reduced.

While covering the nest and exercising, leatherbacks increased their rate of breathing *f* only 2.2 times the resting value. Leatherbacks increased V_T by 36%, while in contrast, green turtles crawling on the beach either decrease or maintain the same tidal volume while active. The leatherback pattern is more typical of vertebrates like mammals and birds that are not experiencing anaerobiosis; leatherbacks exercised strenuously on the beach are probably not pushing the limit of their aerobic capacity whereas green turtles covering their nest probably are at or near their aerobic limit.

Allometric Comparisons. — Allometric equations of respiratory variables are a useful tool for comparing the physiological patterns exhibited by turtles. Allometry also allows one to compare the effects of body mass on different physiological variables from different taxa. We obtained allometric equations for generalized reptilian respiratory physiology from Dejours (1981), Dubach (1981), and Calder (1984), and compared the resultant values (Table 3) to the measured rates and volumes in Table 1. We did not measure the total lung volume (TLV) in our study animals, but the lung volume for leatherbacks measured by Lutcavage et al. (1992) is 25% greater than that predicted by allometric analysis of the lung volumes of other reptiles (Table 3). This result contrasts with the analysis of Lutcavage et al. (1992) that indicated that leatherbacks had measured lung volumes 20-40 % smaller than would be predicted for a green turtle scaled up to the size of a leatherback. Tidal volume in leatherbacks is 11.3 times the predicted value for a similar sized reptile and resting respiratory rate is only 18% of the predicted value for a reptile scaled up to that size. The lung ventilation is 1.7 times the predicted value from allometric analysis. Thus, respiratory variables measured for leatherbacks do not fit the predictions of allometric equations for non-diving generalized reptiles (Dejours, 1981; Calder, 1984).

The large tidal volume and respiratory exchange ratio of these turtles probably helps to provide a large aerobic capacity that is important in their thermoregulation (Paladino et al., 1990), diving behavior and migration (Standora et al., 1984), and their ability to dive to great depths (Eckert et al., 1986). Green turtles also have larger than predicted tidal volumes and lower than predicted respiratory rates (Prange and Jackson, 1976; Jackson and Prange, 1979; Jackson, 1985).

Relationship to Diving. — A number of physiological and anatomical adaptations have been observed in deepdiving, air-breathing animals when compared to their terrestrial or shallow-diving relatives (for reviews see Wood, 1989). These deep diving physiological and anatomical adaptations include:

- High levels of oxygen stores in their tissues primarily due to huge amounts of respiratory pigments stored in metabolically active tissues like muscle;
- High aerobic capacity with enlarged hearts for enhanced circulation and delivery of oxygen to the tissues;
- High tolerance of the respiratory control system and other tissues to hypercapnia (high CO₂ concentration);
- 4. High anaerobic capacity and high tolerance to acidosis;
- A large tidal volume and rapid turnover of air upon surfacing.

This study and others (Rhodin, 1985; Lutcavage et al., 1990; Lutcavage et al., 1992) have shown that leatherback turtles have most of these features and others and are very similar to deep diving mammals in their physiological and anatomical adaptations. Most whales, dolphins, sea lions, and penguins inhale prior to a dive, although some pinnepeds exhale about 20–60% of lung volume prior to a dive (Wood, 1989). The leatherback pattern of breathing is that they inhale prior to diving in a pattern similar to most whales and other deep divers (Paladino, unpublished data).

Some shallow-diving air breathers (sea otters and dolphins) extract and use the oxygen in the lungs during a dive before the pressure causes atelectasis (collapse of alveoli). Jackson (1985) demonstrated that green turtles have a multicameral lung with cartilaginous support of the small airways that prevent collapse when exposed to large hydrostatic pressures. Thus, the lung gases of a deep diving reptile are compressed into the non-respiratory portion of the respiratory tree (bronchi and bronchioles) where little to no gas exchange with the blood will occur. The patency of these non-respiratory passageways under pressure assures that the lung gases will not be trapped in the alveoli where gas exchange could occur and the soft expansible alveolar tissues could expand and rupture due to influx of air from other collapsing bronchi. This lung structure also ensures the air spaces will be easily and readily ventilated when gas exchange is possible at the surface. If the lung passageways collapsed with each dive, air could be easily trapped in different sections of the lung and not readily exchanged. The movement of the lung gases out of the alveoli into the open passageways also reduces the chance that increased oxygen and nitrogen exchange will occur in the alveoli due to increased pressures and cause the associated effects and nitrogen toxicity. We are unaware of data on the structure of leatherback lungs but we expect that they have similar structures to those found in green turtles (Jackson, 1985).

Shallow-diving mammals tend to have a larger than normal lung when compared to other terrestrial and deepdiving mammals. Leatherbacks have a slightly larger than normal total lung volume for a generalized reptile scaled up to that size and this may indicate that some of the oxygen trapped in the lungs may be used during a dive, especially during shallow dives, since these turtles inhale prior to diving. Both leatherbacks and green turtles tend to have higher than predicted tidal volumes for an air-breathing reptile of that size. For air breathers, tidal volumes tend to be 10% of total lung volumes. For example, in humans the average male has a total lung volume of 6 liters and tidal volume averages 0.6 liters or 10% (Wood, 1989). Leatherbacks have a resting tidal volume of 6.2 liters which is more than 28% of the predicted total lung volume. They also appear to have rapid respiration immediately upon surfacing (Paladino, unpublished data). Rapid respiration and a large tidal volume would result in an elevated minute volume. This increased minute volume is typical of diving vertebrates and facilitates a rapid exchange of air in the lung and minimizes the surface time necessary for ventilation (Wood, 1989). Leatherback turtles have a much more "mammalian" respiratory pattern than do green turtles. For example, leatherback turtles adjust both depth and rate of breathing during activity as well as while laying eggs. This suggests that the respiratory control system in leatherbacks is different from that found in green turtles where respiratory frequency was the only mechanism they used to modify ventilation during activity (Jackson, 1985).

Leatherbacks have a high metabolic capacity (Paladino et al., 1990), are very active swimmers (during long distance migrations leatherbacks may travel at an average speed of 70 km per day [Paladino et al., 1993]), and are capable of maintaining high constant body temperatures in cold waters (Frair et al., 1972, Goff and Lien, 1988). These energetic factors require that leatherbacks have a high aerobic capacity to cope with this high oxygen demand. These turtles also dive to depths greater than 500 m (Eckert et al., 1986) where trapped lung gases and gases in solution are pressurized to more than 100 times the value at the surface. The respiratory system of these reptiles meets the conflicting demands of rapid, constant delivery of large quantities of oxygen and removal of carbon dioxide, as well as the constraints on a diving animal of buoyancy and the problems associated with gases in solution under great pressures. This helps leatherbacks to avoid nitrogen narcosis and Caisson's disease which are well documented in the physiology of air breathing diving animals (Wood, 1989). Telemetered dive data for internesting females indicate that the average dive of leatherbacks lasts only about 14 minutes (Eckert et al., 1986) and even on the deepest dives to depths greater than 500 m these turtles do not remain submerged for longer than about 40 minutes.

In conclusion, leatherback turtles have many of the same patterns for control of respiration and adaptations for diving that exist in marine mammals. Leatherbacks have a high aerobic capacity and high tidal volumes and can rapidly move large quantities of air through their respiratory system upon surfacing. They inhale prior to diving and during shallow dives may use this air in the lung as an oxygen store. They have high tissue oxygen stores and normal to above average total lung volume to ensure rapid gas exchange, but unlike mammals they may use lactate as a substrate in the muscle to rapidly replenish glycogen stores depleted during brief bouts of anaerobiosis. This suggests that leatherbacks rely on primarily aerobic metabolism to provide the energy during dives, in a manner similar to marine mammals. A reliance on anaerobic metabolism for an animal that is continually diving would be counterproductive and would require long rest or recovery periods on the surface to replenish glycogen stores and ventilate off excess or stored CO_2 .

Acknowledgments

This project was funded by grants from the National Geographic Society, The Center For Field Studies (Earthwatch), Caribbean Conservation Corporation, and National Science Foundation DCB 9019780. We would like to thank H.G. "Pat" Pattillo, Maria Teresa Koberg, as well as all the Earthwatch volunteers for their help and hospitality. A special thanks to Mario Boza, former Vice Minister of the Costa Rican Ministry of Natural Resources, Energy, and Mines (MIRENEM) and the other personnel at the ministry and Costa Rican national park system for all their help in obtaining international and Costa Rican permits to work on these beaches and for creating a new Costa Rican National Park "Las Baulas de Guanacaste" to protect these magnificent leatherbacks. Jack Woody, Richard Byles, and David Owens helped in obtaining USFWS endangered species research importation and CITES permits for the US. Robert George was especially helpful in the development of physiological protocols for working with leatherbacks. All research protocols were approved by Purdue University and Drexel University Animal Care and Use Review Committees.

LITERATURE CITED

- BERKSON, H. 1966.Physiological adjustments to prolonged diving in the Pacific green turtle. Comp. Biochem. Physiol. 18:101-119.
- BJORNDAL, K.A. 1985. Nutritional ecology of sea turtles. Copeia 1985:736-751.
- BRONGERSMA, L.D. 1969. Miscellaneous notes on sea turtles, II A & B. Proc. K. Ned. Akad. Wet. 1:76-102.
- CALDER, W.A. 1984. Size, Function, and Life History. Cambridge: Harvard University Press, 431 pp.
- DEJOURS, P. 1981. Principles of Comparative Respiratory Physiology. Amsterdam: Elsevier.
- DEN HARTOG, J.C., AND VAN NIEROP, M.M. 1984. A study on the gut contents of six leathery turtles, *Dermochelys coriacea* (Linnaeus) (Reptilia, Testudines, Dermochelyidae) from British waters and from The Netherlands. Zool. Verh. Leiden 209:1-36.
- DEPOCAS, F., AND HART, J.S. 1957. Use of the Pauling oxygen analyzer for measurement of oxygen consumption in open circuit systems and in short lag, closed-circuit apparatus. J. Appl. Physiol. 10:388-392.
- DUBACH, M. 1981. Quantitative analysis of the respiratory system of the house sparrow, budgerigar, and violet eared hummingbird. Respir. Physiol. 46:43-60.
- ECKERT, S.A., NELLIS, D.W., ECKERT, K.L., AND KOOYMAN, G.L. 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during internesting intervals at Sandy Point, St. Croix, U.S. Virgin Islands. Herpetologica 42:381-388.
- FRAIR, W., ACKERMAN, R.G., AND MROSOVSKY, N. 1972. Body temperature of *Dermochelys coriacea*: warm turtle from cold water.

Science 177:791-793.

- GATTEN, R.E., JR. 1985a. Activity metabolism of lizards after thermal acclimation. J. Therm. Biol. 10:209-215.
- GATTEN, R.E., JR. 1985b. The uses of anaerobiosis by amphibians and reptiles. Amer. Zool. 25:945-954.
- GATTEN, R.E., JR., CONGDON, J.D., MAZZOTTI, F.J., AND FISCHER, R.U. 1991. Glycolysis and swimming performance in juvenile American alligators. J. Herpetol. 25:406-411.
- GLEESON, T.T. 1991. Patterns of metabolic recovery from exercise in amphibians and reptiles. J. Exp Biol. 160:187-207.
- GOFF, G.P., AND LIEN, J. 1988. Atlantic leatherback turtles, *Dermochelys coriacea*, in cold water off Newfoundland and Labrador. Can. Fld. Nat. 102:1-5.
- GREER, A.E., LAZELL, J.D., AND WRIGHT, R.M. 1973. Anatomical evidence for a countercurrent heat exchanger in the leatherback turtle (*Dermochelys coriacea*). Nature 244:181.
- GUPPY, M., HILL, R.D., SCHNEIDER, R.C., QVIST, J., LIGGINS, G.C., ZAPOL, W.M., AND HOCHACHKA, P. 1986. Microcomputer-assisted metabolic studies of voluntary diving of Weddell seals. Am. J. Physiol. 250:R175-187.
- GUYTON, A.C. 1986. Textbook of Medical Physiology. 7th Edition. Philadelphia, PA: W.B. Saunders Co., 1057 pp.
- JACKSON, D.C. 1985. Respiration and respiratory control in the green turtle, *Chelonia mydas*. Copeia 1985:664-671.
- JACKSON, D.C., AND PRANGE, H.D. 1979. Ventilation and gas exchange during rest and exercise in adult green turtles. J. Comp. Physiol. 134:315-319.
- LUTCAVAGE, M.E., BUSHNELL, P.G., AND JONES D.R. 1990. Oxygen transport in the leatherback sea turtle *Dermochelys coriacea*. Physiol. Zool. 63:1012-1024.
- LUTCAVAGE, M.E., BUSHNELL, P.G., AND JONES, D.R. 1992. Oxygen stores and aerobic metabolism in the leatherback sea turtle. Can. J. Zool. 70:348-351.
- MORTIMER, J.A. 1982. Feeding ecology of sea turtles. In: Bjorndal, K.A. (Ed.). Biology and Conservation of Sea Turtles. Washington,

DC: Smithsonian Institution Press, pp. 103-109.

- MROSOVSKY, N., AND PRITCHARO, P.C.H. 1971. Body temperatures of Dermochelys coriacea and other sea turbles. Copera 1971;524–531.
- OWENS, D.W., AND RUIZ, G.J. 1980. New methods of obtaining blood and cerebrospinal fluid from marine turtles. Herpetologica 35:17-30.
- PALADINO, F.V., AND KING, J.R. 1984. Thermoregulation and oxygen consumption during terrestrial locomotion by white-crowned sparrows, *Zonotrichia leucophrys gambelii*. Physiol Zool. 57:226-236.
- PALADINO, F.V., O'CONNOR, M.P., AND SPOTILA, J.R. 1990. Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. Nature 344:858-860.
- PALADINO, F.V., AND SPOTILA, J.R. 1993. Does the physiology of large living reptiles provide insights into the evolution of endothermy and paleophysiology of extinct dinosaurs. In: Rosengerg. G.D., and Wolberg, D.L. (Eds.). Dinofest Proceedings. Paleontological Society Special Publ. 7, University of Tenn. Press. Knoxville, pp. 261-274.
- PRANGE, H.D., AND JACKSON, D.C. 1976. Ventilation, gas exchange and metabolic scaling of a sea turtle. Respir. Physiol. 27:369-377.
- RHODIN, A.G.J. 1985: Comparative chondro-osseous development and growth of marine turtles. Copeia 1985:752-771.
- STANDORA, E.A., SPOTILA, J.R., KEINATH, J.A., AND SHOOP, R.C. 1984. Body temperatures, diving cycles, and movement of a subadult leatherback turtle, *Dermochelys coriacea*. Herpetologica 40:169-176.
- VAN TIENHOVEN, A. 1983. Reproductive Physiology of Vertebrates. 2nd Edition. Ithaca, NY: Cornell University Press, 491pp.
- WEINHEIMER, C.J., PENDERGAST, D.R., SPOTILA, J.R., WILSON, D.R., AND STANDORA, E.A. 1982. Peripheral circulation in *Alligator mississippiensis*: effects of diving, fear, movement, investigator activities, and temperature. J. Comp. Physiol. 148:57-63.
- Wood, S.C. 1989. Comparative Pulmonary Physiology Current Concepts. (Lung Biology in Health and Disease, Vol. 39). New York: Marcel Dekker Inc., 854 pp.

Received: 21 September 1995. Accepted: 22 March 1996.