Respiration in Neonate Sea Turtles

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The pattern and control of respiration is virtually unknown in hatchling sea turtles. Using incubator-raised turtles, we measured oxygen consumption, frequency, tidal volume, and minute volume for leatherback (*Dermochelys coriacea*) and olive ridley (*Lepidochelys olivacea*) turtle hatchlings for the first six days after pipping. In addition, we tested the hatchlings' response to hypercapnic, hyperoxic, and hypoxic challenges over this time period. Hatchling sea turtles generally showed resting ventilation characteristics that are similar to those of adults: a single breath followed by a long respiratory pause, slow frequency, and high metabolic rate. With hypercapnic challenge, both species responded primarily by elevating respiratory frequency via a decrease in the non-ventilatory period. Leatherback resting tidal volume increased with age but otherwise, neither species' resting respiratory pattern nor response to gas challenge changed significantly over the first few days after hatching. At the time of nest emergence, sea turtles have achieved a respiratory pattern that is similar to that of actively diving adults.

Keywords

leatherback; *Dermochelys*; olive ridley; *Lepidochelys*; Playa Grande; Costa Rica; ventilation; ontogeny; nest; neonate

Introduction

Although sea turtle hatchlings face some unique respiratory challenges, the pattern and control of respiration in hatchlings remains poorly studied. Sea turtles lay their eggs in a beach nest that they cover with up to a meter of sand. This environment limits gas exchange between the nest and the atmosphere, and neonate sea turtles therefore hatch into a hypoxic and hypercapnic nest environment (Prange and Ackerman 1974, Ackerman 1977, Clusella-Trullas 2000). Climbing upward through the sand, the hatchlings emerge at the beach surface 4 to 7 days after pipping (Godfrey and Mrosovsky 1997). Immediately after emergence, the hatchlings crawl to the sea and begin a life of active diving. This timeline of changing environments and respiratory demands makes sea turtle hatchlings interesting models for studying reptilian respiratory physiology. Moreover, the leatherback turtle (*Dermochelys coriacea*) reaches

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superlative size as an adult (Paladino et al. 1990); hatchlings of this species might be expected to exhibit similar respiratory adaptations as their adult counterparts, or they might develop similar respiratory features with increasing age and size.

Although the respiratory physiology of adult leatherback (Paladino et al. 1996), green (*Chelonia mydas*; Jackson and Prange 1979, Jackson et al. 1979, Jackson 1985), and loggerhead (*Caretta caretta*; Lutz and Bentley 1985, Lutcavage et al. 1987, Lutcavage et al. 1989) turtles has been investigated, there have been few studies of respiration in hatchlings. Prange and Ackerman (1974) studied the oxygen consumption of green turtle hatchlings, and Lutcavage and Lutz (1986) report hatchling respiratory frequencies, but there are no other studies of sea turtle hatchling ventilatory pattern. Therefore, one goal of the present study was to provide baseline information on ventilatory pattern in leatherback and olive ridley (*Lepidochelys olivacea*) sea turtle hatchlings.

We also addressed two questions regarding ventilation in hatchling sea turtles. First, we investigated how neonate sea turtles respond to environmental changes in carbon dioxide loading and hypoxia. In response to increased inspired CO₂, adult green turtles primarily increase respiratory frequency (Jackson 1985) rather than tidal volume. Similarly, adult leatherback turtles increase V_E in response to activity primarily by means of increased respiratory frequency (Paladino et al. 1996). Fossorial (burrow-dwelling) mammals tend to exhibit blunted responses to CO₂; however, the response typically involves a decrease in respiratory frequency and an increase in tidal volume (Boggs 1992, Walker et al. 1985). Neonate sea turtles hatch in a “fossorial” environment, yet must anticipate a life of diving. We therefore predicted that sea turtle hatchlings would exhibit hypercapnic responses similar to those of adult sea turtles. Second, we examined the breath holding behavior of sea turtle hatchlings. While the general ventilatory pattern of reptiles includes these non-ventilatory periods, or apneas, sea turtle hatchlings might prepare for a life of diving by increasing the duration of breathholding as they get closer to emergence at the sand surface. This development of increasingly long apneas occurs in neonatal elephant seals, and may be necessary before these seals can dive successfully (Blackwell and LeBoeuf 1993, Castellini et al. 1994, Falabella et al. 1999). The present study aims to describe the respiratory pattern of leatherback and olive ridley hatchlings, and to investigate changes in ventilatory pattern and control of respiration over the first several days after hatching.

Methods

Animals

We obtained 18 leatherback (*Dermochelys coriacea*) and 22 olive ridley (*Lepidochelys olivacea*) hatchlings from eggs which were collected as they were laid by turtles at Playa Grande, Costa Rica and we subsequently incubated the eggs in a laboratory. Playa Grande is a major nesting beach for leatherback turtles in the Pacific Ocean (Steyermark et al. 1996, Reina et al. 2002) and it also serves as a nesting beach for a population of olive ridley turtles that do not nest in arribadas (coordinated mass nestings), but rather nest individually. We incubated eggs at 31±0.5 °C in Styrofoam, thermal airflow Hova-Bators (G.Q.F. Mfg. Co., Savannah, GA, USA) that were filled with sand to approximately 2/3 full (Bilinski et al. 2001). A 24-gauge copper-constantan (Cu-Cn) thermocouple placed in the sand in the center of each incubator measured temperature (±0.05 °C). At this incubation temperature all leatherback hatchlings develop into females (Binckley et al. 1998), as do most olive ridleys (Wibbels 2003). Sand was maintained at 5% moisture (measured gravimetrically). We did not measure oxygen partial pressure in incubators, but it was probably similar to atmospheric because incubators were opened every day and were not airtight.

Animals were in complete darkness, both during testing and while in incubators, and were released on the beach at night after the completion of measurements. This research was conducted under a scientific research permit issued by the Ministerio de Ambiente y Energía (MINAE), Costa Rica, and animal care protocols approved by Indiana-Purdue University.

Measurement of Ventilatory Behavior and Oxygen Consumption

We used whole body plethysmography by the closed circuit method to measure respiratory frequency and tidal volume (V_T). Animals were tested in a round Lucite chamber (710 mL volume) containing an inlet port for the administration of test gases. We closed the outlet port during testing but opened it to flush gases out of the chamber between experiments. The chamber was connected to one side of a pressure transducer (Validyne DP45, Validyne Engineering, CA, USA) with a sensitivity of ± 2 cmH₂O, referenced to atmosphere. As the animal breathed, the transducer recorded swings in chamber pressure and then processed them to a voltage signal. This signal was amplified (Validyne CD15) and filtered with a band pass filter which allowed 1–20 Hz signals to pass through. Respiratory frequency was calculated from this signal in units of breaths min⁻¹ and the correspondence of respiratory frequency by plethysmography to more direct measurements is generally excellent. Furthermore, visual inspection of turtles during plethysmographic measurement of respiratory frequency revealed excellent correlation with breathing in our experimental animals. We measured tidal volume by examining the excursion of the voltage signal recorded on a strip chart recorder (Linear Instruments, Reno NV). There are problems with the accuracy of whole-body plethysmography to measure absolute tidal volume (Subramanian et al. 2002), particularly in ectotherms which provide a small differential between ambient and body temperatures. However, the method of estimating tidal volume and a corresponding minute ventilation (V_E [Volts min⁻¹] = frequency [breaths min⁻¹] $\times$ tidal volume [volts breath⁻¹]) permits relative comparisons between and within individual animals undergoing different treatments. Therefore, tidal volumes and minute volumes are presented as voltages and should be considered relative measurements.

Generally we tested turtles on the first night after pipping the eggshell. Thereafter, we tested them every 1–2 days until ready for release (4–6 days). We placed turtles in the plethysmograph and measured oxygen consumption for 10 min before beginning other experimental protocols. We measured the fractional content of O₂ continuously by sampling recirculating gas that passed through an oxygen sensor (Qubit S102 O₂ sensor, Qubit Systems, Kingston, Ontario) after being dried and scrubbed of CO₂ using drierite and ascarite. Oxygen concentration did not generally decrease below 20% during this time period. Oxygen consumption was calculated from the change in the chamber volume of oxygen during the 10 min of measurement and was corrected to standard temperature and pressure. Resting breathing pattern was then measured for 10 min by plethysmography. At the conclusion of this period, we flushed a gas (hypoxia [8% O₂/92% N₂], hypercapnia [5% CO₂/95% O₂], or hyperoxia [100% O₂]) through the chamber, quickly resealed it, and after 10 min of acclimation, again measured ventilatory pattern by plethysmography for a period of 10 min. Hypoxia was administered without accompanying hypercapnia in order to investigate the action of the hypoxic sensor without any input from that for hypercapnia. Similarly, hypercapnia was administered with balance oxygen in order to wash out the hypoxic sensor and focus on the effects of the hypercapnic sensor.

Mass could not be accurately measured on days in which hatchlings were still partially inside of their eggs. Further, hatchlings do not begin feeding until after entering the ocean. Therefore, we only measured mass (using a balance accurate to 0.01 g) on the final day of testing for each animal (immediately before release). Chamber temperature did not vary by species or day. We analyzed data using S-PLUS (Insightful Corp., Seattle, WA, USA) and set $P = 0.05$ to determine significance of results. Significant responses to gas challenge were detected using a Wilcoxon Signed Rank test. Because individual animals were tested at different time points, changes in

respiratory patterns or response with age were analyzed using a randomization script written in S-PLUS. Briefly, it sampled individuals and randomly reordered the time points associated with values for that individual. A least squares regression slope was calculated based on all individuals with their reordered time points. Randomization was repeated 1000 times, and the observed regression slope from the data was compared to the distribution of 1000 randomized regressions to determine significance. Data are presented as mean $\pm$ SE.

Results

Resting Breathing

Leatherback hatchlings had a mean mass of 38.03 ± 0.85 g and olive ridley hatchlings had a mean mass of 15.32 ± 0.29 g. Hatchlings of both species exhibited a resting breathing pattern of single breaths followed by long pauses (Fig 1 & 2). On the day of release, leatherbacks had a mean frequency of 1.45 ± 0.22 breaths min^{-1} (range 0.39 to 2.80) and oxygen consumption of 8.14 ± 0.48 mL h^{-1} (range: 5.39 to 10.78). Olive ridley turtles had a mean frequency of 1.49 ± 0.17 breaths min^{-1} (range: 0.44 to 2.72) and oxygen consumption of 2.03 ± 0.24 mL h^{-1} (range: 0.34 to 3.21). During resting breathing on the day of release, leatherback respiratory pauses lasted 52.25 ± 8.64 sec, reaching as long as 185 sec. Resting olive ridleys exhibited respiratory pauses lasting 52.77 ± 8.68 sec, reaching a maximum of 372.50 sec in duration. The instantaneous breathing frequency for resting leatherbacks was 0.67 ± 0.03 breaths sec^{-1} while that of olive ridley hatchlings was 0.58 ± 0.03 breaths sec^{-1} .

Resting Respiratory Pattern and Age

Over the first 5 days after pipping, leatherback hatchlings showed a change in resting respiratory pattern (Fig 3). While respiratory frequency did not change significantly (and trended slightly negative), V_T ($r^2 = 0.399$, $P = 0.002$) increased significantly with age. Over this time period, V_E and oxygen consumption did not increase significantly with age ($P > 0.05$). Olive ridleys, however, exhibited no relationship between frequency, V_T , V_E , or O_2 consumption with age (Fig 4). Apnea duration did not vary significantly with age for either species (Leatherback: $P = 0.128$; Olive Ridley: $P = 0.172$). Instantaneous frequency also did not change with age for leatherbacks ($P = 0.777$) or olive ridleys ($P = 0.158$).

Response to Hypoxic, Hyperoxic, and Hypercapnic Challenge

For general response to gas challenges, data presented are only from the last day of measurement for each individual turtle. The response to hyperoxia in both species was non-significant for the measured variables (Table 1). Under hypoxic stimulus, leatherbacks did not show significant changes to breathing pattern. Olive ridleys, however, responded with increased frequency ($P = 0.0312$, accomplished by a 27% decrease in the non-ventilatory period [$P = 0.016$]) which was offset by a decrease in V_T ($P = 0.0312$) such that V_E was unaltered. Hatchlings of both species responded most strongly to the hypercapnic challenge with large and significant increases in frequency (leatherbacks, $P = 0.0312$; olive ridleys, $p = 0.008$). This was accomplished by a decrease in the non-ventilatory period (significant for olive ridleys, -84% , $P = 0.013$). This resulted in a significantly increased V_E for olive ridley hatchlings ($P = 0.019$). Instantaneous frequency was not significantly changed from resting values by any gas challenge for either species. Neither the leatherback nor olive ridley response to respiratory challenge varied significantly with age for any of the gases administered.

Discussion

The respiratory pattern of reptiles is characterized by a long respiratory pause followed by either a single breath or a burst of breaths (Wood and Lenfant 1976, Glass and Wood 1983). Like their adult counterparts, the hatchling leatherback and olive ridley turtles of this study

generally displayed single breaths followed by apneas. Like many other reptiles, the duration of this non-ventilatory period was much greater than that of the ventilatory period. The reptilian pattern of breathing may have preadapted sea turtles to a life of diving as suggested by Lutz and Bentley (1985). Elephant seals have been shown to increase apnea duration during development, and it has been suggested that such development is required before seals can achieve the diving/breath-holding ability characteristic of adults (Blackwell and LeBoeuf 1993, Castellini et al. 1994). However, the sea turtle hatchlings in this study showed no significant increase in apnea duration with age.

Diving, air-breathing vertebrates tend to have large tidal volumes for their size, a property which facilitates a rapid turnover of gases while surfacing and quick return to diving (Kooyman 1973, Lutz and Bentley 1985, Jackson 1985). At the time of release, corresponding to the time of emergence from the nest onto the beach (day 3–6), both species exhibited respiratory frequencies more than 90% lower than those predicted by allometric equations for reptiles given by Dejours (1981; Fig 5). At the same time, leatherbacks consumed oxygen at a higher rate than predicted allometrically for reptiles or turtles (equations from Bennett and Dawson 1976) and Olive ridleys consumed oxygen at a higher rate than predicted for turtles, and at a similar rate to that predicted for reptiles in general (Fig 5). The allometric equation available for turtles is for 20 °C; however, using a conservative estimate of 3 for Q_{10} , both species still have higher than predicted rates of oxygen consumption. Absolute tidal volume could not be measured accurately in this study, but the low frequencies and high O_2 consumption suggest relatively high tidal volumes. Low respiratory frequencies are combined with large tidal volumes in adults (Paladino et al. 1996). Thus at the time of sand emergence, sea turtles have already achieved a respiratory frequency, and possibly tidal volume, that would prepare them for a life of diving. Also at the time of emergence from the sand, sea turtle hatchlings have higher than predicted oxygen consumption rates, which apparently remain high through adulthood (Paladino et al. 1996, Prange and Ackerman 1974). These high metabolic rates should still be considered resting rates, and not the high rates associated with post beach emergence frenzy (Wyneken 1997), although these turtles may have higher than predicted metabolic rates because of the rapid growth experienced by juvenile leatherbacks. The increase in V_T with age in leatherbacks may be a result of unfolding from the tucked position in the egg, as oxygen consumption did not increase in parallel with V_T .

Although substantial variation sometimes precluded statistically significant responses to inspired gas challenges, the directions of the observed responses were generally in line with expectations. Specifically, both species showed trends or significant increases in f in response to hypoxia. Hypercapnia elicited the strongest ventilatory response, which was primarily mediated via an increase in respiratory frequency, a response pattern typical of reptiles (Vitalis and Milsom 1986, Wang et al. 1998), diving mammals (Kooyman 1973), and a fossorial amphisbaenian (Abe and Johansen 1987), but not fossorial mammals (Boggs 1992, Walker et al. 1995). The increase in frequency was achieved by a reduction of the non-ventilatory period while keeping instantaneous frequency unchanged. This is common for reptiles, as maintaining the instantaneous frequency constant minimizes the work of breathing (Vitalis and Milsom 1986). Adult green turtles (Jackson et al. 1979) and leatherback turtles (Paladino et al. 1996) also increased V_E primarily via an increase in frequency. The absence of a significant V_T response may indicate that hatchlings are using near total vital capacity (Jackson et al. 1979). Olive ridley hatchlings showed a greater V_E response to hypercapnia than leatherback hatchlings, a phenomenon that may be related to the shallower nests of olive ridley turtles. Alternatively, it could be due to lifestyle differences, as leatherback hatchlings are more likely to spend time diving than green or loggerhead hatchlings (Wyneken 1997) and presumably olive ridleys as well.

Limitations

A great deal of variability was observed in both species. This variability could be natural or as a result of the study design. For example, recording periods may not have been long enough to capture the full response to inspired gases. For this reason, and due to small sample sizes available, the non-significant relationships found may not describe the natural state well. Hatchlings were incubated and raised in a near normoxic environment, which could have affected the results of this study. Qualitatively, however, it seems likely that basic respiratory patterns seen in this study, including low f and high metabolic rate, along with response to hypercapnia achieved through decreases in the non-ventilatory period, are representative of wild animals. Moreover, these patterns are similar to those described for other reptiles and sea turtles in particular.

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Fig 1.
Representative traces showing respiratory pattern of leatherback hatchlings under condition of normoxia, hypoxia, and hypercapnia.

Fig 2.
Representative traces showing respiratory pattern of olive ridley hatchlings under condition of normoxia, hypoxia, and hypercapnia.

Fig 3.

Resting breathing pattern of leatherback hatchlings over time. There is a significant relationship between V_T ($y = 2.58x + 7.78$, $r^2 = 0.22$) and age.

Fig 4. Resting breathing pattern of olive ridley hatchlings over time. There are no significant relationships between f , V_T , V_E , or oxygen consumption and age.

Fig 5.

Comparison of observed respiratory frequency and oxygen consumption with predicted values based on allometric equations for reptiles and turtles. Mass and respiratory variables were measured on day of release. Mean mass of leatherbacks was 38.03 ± 0.85 g; mean mass of olive ridleys was 15.32 ± 0.29 g ($n = 13$ for both species). Frequency equation ($\text{freq} = 20.6M^{-0.04}$; M = mass in kg) is from Dejours (1981). Oxygen consumption equations for reptiles at 30°C ($V_{\text{O}_2} = 0.278m^{0.77}$) and turtles at 20°C ($V_{\text{O}_2} = 0.066m^{0.86}$; m = mass in g) are from Bennett and Dawson (1976).

Table 1
Ventilatory response of sea turtle hatchlings to gas challenges.

Species	Challenge	n	Δf (%)	ΔV_T (%)	ΔV_E (%)
<i>D. coriacea</i>	Hyperoxia	5	13.93 $\pm$ 17.74	-24.05 $\pm$ 10.84	-10.78 $\pm$ 21.65
	Hypoxia	7	24.80 $\pm$ 19.68	19.15 $\pm$ 29.79	39.95 $\pm$ 39.14
	Hypercapnia	6	209.51 $\pm$ 108.5*	-37.30 $\pm$ 8.10	181.35 $\pm$ 99.30
<i>L. olivacea</i>	Hyperoxia	7	37.16 $\pm$ 18.60	-5.83 $\pm$ 20.28	23.55 $\pm$ 29.12
	Hypoxia	7	57.84 $\pm$ 19.65*	-39.11 $\pm$ 89.00*	-1.51 $\pm$ 15.04
	Hypercapnia	8	517.74 $\pm$ 178.5*	15.09 $\pm$ 41.72	1031.41 $\pm$ 338.31*

Data are % change from resting measurements. Mean $\pm$ SE are presented.

* Statistically significantly different from zero.