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Rhythmic Throat Oscillations in Nesting Green Turtles (*Chelonia mydas*)

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ABSTRACT. – Female green turtles (*Chelonia mydas*) were monitored for signs of throat movements/oscillations when attempting to nest at Ascension Island in the S5outh Atlantic. Throat oscillations occurred during all stages of the nesting process, with the mean frequency ranging from 10.9 to 36.1 oscillations/min, while the mean breathing rate for different stages during nesting activity ranged from 1.3 to 2.8 breaths/min.

Among extant vertebrates, animals can be classified according to their lung ventilation mechanism: those that ventilate by aspiration breathing, those that use a buccal pump, and those that use both mechanisms (Brainerd 1999). Mammals, birds, most lizards, snakes, turtles, and crocodilians are aspiration breathers, expanding their thorax to create negative pressure, thus drawing air into the lungs. Air-breathing fish and some amphibians are buccal pump breathers, which move air in and out of the lungs by expanding and compressing the buccal cavity (Brainerd 1999). Until recently it was thought that amniotes used aspiration breathing alone, but recent work on some lizards has shown that the buccal pump can complement aspiration breathing during exercise and when higher ambient temperatures are experienced, possibly

because of an associated increase in metabolic rate and increased demand for oxygen (Al-Ghamdi et al. 2001; Owerkowicz et al. 2001).

Studies of marine turtles have predominantly focused on their behavior and physiology while on land as these studies are generally less challenging logistically than monitoring turtles at sea. However, while a wealth of data exists from the nesting beach, rhythmic throat movements carried out by turtles during nesting activities have been little studied. While on land or submerged, marine turtles maintain a rhythmic movement of the throat, a behavior that in turtles has been assumed to aid lung ventilation (Agassiz 1857) or play an olfactory role (Walker 1959; Druzisky and Brainerd 2001). Among marine turtles, buccal oscillations have been shown to increase in frequency when turtles orient towards a food source (McCutcheon 1943). Recent work on the freshwater turtle *Platysternon megacephalum* using X-ray videography and airflow measurements has shown that buccal movements carried out above water are not involved in lung ventilation (Druzisky and Brainerd 2001). In conjunction with these studies and in line with the presence of intricate olfactory and vomeronasal epithelia in marine turtles, an elaborate chemical sense is likely (Beuerman 1975, 1977; Saito et al. 2000).

As there is a paucity of information concerning the role of throat oscillations in marine turtles, and furthermore, any work that has been carried out to date has been anecdotal (Walker 1959), invasive, and/or carried out under laboratory conditions (McCutcheon 1943), we set out to examine the natural occurrence of rhythmic throat oscillations in marine turtles. Green turtles nesting on Ascension Island were chosen for this study, as it has been hypothesized that they may use wind-borne cues to navigate to their breeding area (Luschi et al. 2001). It seemed appropriate therefore that we monitor these turtles, using a noninvasive technique, while they attempted to nest.

Methods. — The study was carried out on Long Beach, Ascension Island (7°57'S, 14°22'W) in the South Atlantic Ocean, during May 2000 and January 2002. The behavior of 79 different adult turtles was monitored using 2 observation techniques. To minimize distressing turtles when they were most easily disturbed (during their ascent and descent of the beach), turtles were observed using a night vision scope (Kite MK-4, Pilkington Optronics) mounted with an infrared light. The observer stood 20 m away from the turtle (the minimum focusing distance). We classified "throat movements" as the rhythmic distension and compression of the throat that occurred between each breath. "Breathing" was classified as opening of the mouth accompanied by elevation of the head and an audible expiration/inspiration. In total, 29 different turtles were monitored for a period of 5 min using the night vision scope, and the number of breaths and throat oscillations counted. Activities were classified into 4 stages: ascending the beach to nest; ascending the beach to attempt to nest,

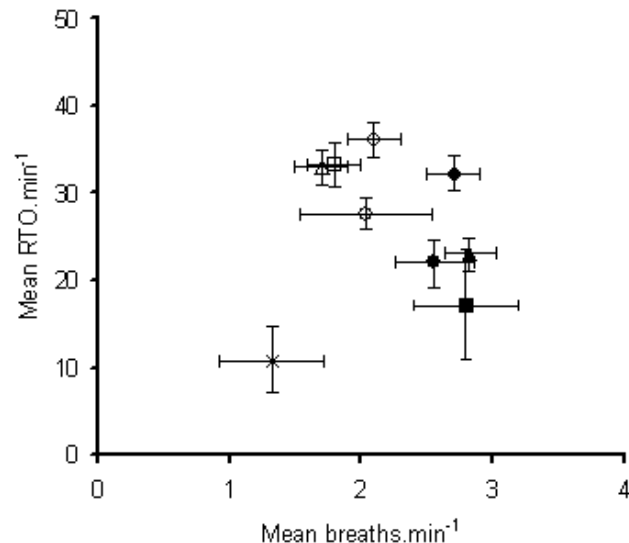


Figure 1. Relationship between the mean breathing rate and the mean rhythmic throat oscillation (RTO) rate in all 9 nesting stages. Error bars are ± 1 SD. $\diamond$ Ascent to attempt, $\square$ Ascent to nest, $\circ$ Digging body pit, $\bullet$ Digging egg chamber, $\times$ Egg deposition, $\blacksquare$ Covering eggs, $\blacktriangle$ Camouflaging the nest, $\blacklozenge$ Descent from nest, $\triangle$ Descent from attempt.

but not successful; descending the beach having nested; descending the beach having failed to nest.

While digging of the body pit and egg chamber, egg deposition, covering of eggs, and camouflaging of the nest (see Miller 1997, for review), the buccal/cervical region of turtles were partially obscured by shadow. Therefore, during each of these further 5 stages, the observer recorded throat movements at a distance of 5 m using a weak light focused on the buccal region. No discernable effect on turtle behavior was observed. For a period of 5 min, breathing and throat movement rates were monitored during each nesting stage. A total of 50 different turtles were observed using this method, 10 for each stage (digging the body pit, digging the egg chamber, egg deposition, covering the eggs, and camouflaging the nest).

Results. — The mean frequency of throat movements recorded during the 9 nesting stages ranged from 10.9 to 36.1 oscillations/min, and the mean breathing rate from 1.3 to 2.8 breaths/min (Fig. 1). During egg deposition, the rates of breathing and throat oscillations were significantly lower than during all other stages (ANOVA throat oscillation rate: $F_{1,78} = 11.91$, $p < 0.001$; post hoc Tukey test, breathing rate: $F_{1,78} = 4.34$, $p < 0.001$; post hoc Tukey test). A qualitative observation during this study was that breathing only took place when turtles paused briefly during locomotion, as opposed to throat oscillations, which occurred both during locomotion and when the turtles were stationary.

Discussion. — Unlike the box turtle *Terrapene carolina*, which ventilates during locomotion (Landberg et al. 2001), green sea turtles monitored during this study carried out vigorous periods of activity (crawling, digging, throwing of sand) without breathing, alternating regularly

with periods of inactivity, when they breathed. Two explanations of this phasic activity are: 1) the turtle works to exhaustion during each episode, and then stops to recover, or 2) because some of the same muscles are involved with both breathing and activity, the turtle cannot breathe and move simultaneously (Jackson and Prange 1979). During this study, throat oscillations occurred both during periods of locomotion and when turtles were stationary.

During the stages prior to egg deposition or when the turtle had not successfully nested, breathing frequency was generally low. Stages subsequent to egg deposition have been described as metabolically expensive, with energy metabolism increasing to 10 times the standard resting level (Jackson and Prange 1979) in the green turtle. In the leatherback turtle (*Dermochelys coriacea*) breathing frequency has been observed to increase from 1.0 to 3.3 breaths/min between egg deposition and sand throwing phases (Lutcavage et al., 1990; Paladino et al. 1990). The lowest breathing rates in our study were recorded during egg deposition. One explanation for this trend could be that an increase in intracoelemic pressure may be enhanced by the contraction of respiratory muscles when the glottis is closed. This may augment peristaltic movement of the oviduct. Another explanation may be that egg laying is not a strenuous activity, hence incurring a lower oxygen demand. If throat oscillations are involved in lung ventilation, the observed drop in frequency could be attributable to the theories proposed above. However, if throat oscillations are involved in olfaction, during laying the predominant odor would likely be that of the eggs, making the use of olfaction at this stage redundant.

Apart from the egg deposition stage, similar rates of throat oscillations were observed during all other stages of nesting. Although this study made no attempt to explain the functional significance, we have provided the first noninvasive description of throat oscillations in marine turtles. While it would be nearly impossible to carry out pneumotachography readings on protected marine turtles within the natural environment, further work involving an alteration of the ambient odor and monitoring subsequent changes in the rate of throat oscillations may enable the functional significance of throat oscillations of marine turtles while on land to be determined.

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