Simultaneous measurements of breaths and energy expenditure reveal the dive tactics of sea turtles.
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Abstract
Air-breathing divers are assumed to have evolved to apportion their time between surface and underwater periods to maximize the benefit gained from diving activities. However, whether they change their time allocation depending on the aim of the dive is still unknown. This may be particularly crucial for ‘surfacers’ because they dive for various purposes in addition to foraging. In this study, we counted breath events at the surface and estimated oxygen consumption during resting, foraging, and other dives in 11 green turtles (Chelonia mydas) in the wild. Breath events were counted by a head-mounted acceleration logger or direct observation based on an animal-borne video logger, and oxygen consumption was estimated by measuring overall dynamic body acceleration. Our results indicate that green turtles maximized their submerged time, following this with 5-7 breaths to replenish oxygen for resting dives. However, they changed their dive tactic during foraging and other dives; they surfaced without depleting their oxygen content, followed by only a few breaths for effective foraging and locomotion. These dichotomous surfacing tactics would be the result of behavioral modifications by turtles depending on the aim of each dive.

Keywords: biologging, chelonia mydas, diving physiology, metabolism, respiratory

Introduction
For air-breathing divers, underwater activity is constrained by the available amount of oxygen stored in the body. Under such physiological constraints, they are assumed to have evolved to apportion their time between surface and underwater periods to maximize the benefit gained from activities such as feeding, predator avoidance, and mating [1]. Therefore, from an ecological point of view, it is essential to understand dive-induced respiratory patterns in air-breathing divers. To understand such diving strategies/tactics of air-breathing animals, it is essential to measure both the energy expenditure during a dive and subsequent respiratory performance at the surface.

Sea turtles are ectothermic marine animals and have well-adjusted physiological functions for prolonged dives (reviewed by [2, 3]). Briefly, they have a considerably slower metabolism than do diving mammals and birds, but it is affected by water temperature and activity level [4-6]. They begin a voluntary dive with a level of oxygen in their body that approaches saturation, and they complete it at a level approaching depletion [7-8]. Their highly elastic reinforced lungs and high lung oxygen diffusion capacity allow them to reduce the time spent at the surface [9-10].

In this study, we simultaneously counted breath events at the surface and estimated oxygen consumption during resting, foraging, and other dives in green turtles (Chelonia mydas) in the wild. The objectives of this study were to clarify how green turtles manage their energy expenditure during a dive and subsequent respiratory patterns based on the purpose of the dive (resting, foraging, and other) under natural conditions and to determine which dive tactics they employ.

Materials and Methods
Study area and experimental animals
This study was conducted around Iriomote Island, Okinawa, Japan (24°20’N, 123°50’E). We used 11 juvenile green turtles that were hand captured by a local fisherman with the permission of the Okinawa Prefecture (Permission No. 22-3, 23-2, 24-4).
Breath events were counted using a head-mounted acceleration logger or direct observation based on an animal-borne video logger, and oxygen consumption was estimated by measuring overall dynamic body acceleration (ODBA) and using equations developed by Enstipp et al. [11] and Halsey et al. [12] to convert ODBA to oxygen consumption.

**Instruments**

We used various types of data loggers. To monitor breathing behavior, we used a small acceleration data logger (M190L-D2GT, Little Leonardo Co., Tokyo, Japan) or a video data logger (GoPro HD®, Woodman Labs, CA, USA) with a custom-made waterproof case (Logical Product Co., Fukuoka, Japan). To measure depth and respiration, we used a multi-sensor data logger (W1000-3MPD3GT, Little Leonard Co or LP-KUBL1101, Logical Product Co). For the detail in experimental protocol, see Okuyama et al. [13]

**Results**

A total of 555 dive data sets (dive duration, ODBA, and NB) by 11 immature green turtles, were extracted. The NB was significantly different among resting dives (N = 177, mean ± S.D. = 5.9 ± 2.5), foraging dives (N = 113, 2.1 ± 1.6), and other dives (N = 394, 2.3 ± 2.2) (ANOVA, F = 171.0, P < 0.001). Video observation and depth profiles showed that during resting dives, individuals took breaths without continuing to swim, although they often rotated. During this rotating behavior, the turtles kept their heads down and appeared to be engaging in locating/searching behaviors for a resting place before surfacing. During foraging and other dives, meanwhile, the turtles took breaths while continuing to feed or swim.

As for oxygen consumption per dive (\( V_{O2} \)), values were estimated at 14.54 ± 3.70, 4.01 ± 2.31, and 5.10 ± 4.57 ml kg\(^{-1}\) using Halsey's equation during resting, foraging, and other dives, respectively. Using Enstipp's equation, these values were 6.34 ± 1.69, 1.56 ± 0.82, and 2.07 ± 1.91 ml kg\(^{-1}\), respectively. There were significant differences in oxygen consumption per dive among the dives estimated by both Halsey's (ANOVA, F = 34.8, P < 0.001) and Enstipp's equations (ANOVA, F = 38.4, P < 0.001).

The LMM analysis revealed that NB increased significantly with larger energy expenditures as estimated by both Halsey's (\( X^2 = 114.7, P < 0.0001 \)) and Enstipp's equations (\( X^2 = 94.6, P < 0.0001 \)), but not with water temperature (\( X^2 = 0.00, P = 1 \), for Halsey's equation only). The activity state (i.e. resting, foraging, or other dive) also significantly affected NB using both Halsey's (\( X^2 = 17.7, P < 0.001 \)) and Enstipp's equations (\( X^2 = 13.8, P < 0.01 \)).

**Discussion**

Surfacers are expected to maximize the ratio of submerged to surface time during dives so as to minimize surface time [1]. In our study, green turtles also maximized the submerged time during resting dives. However, they changed their dive tactic during foraging and other dives; they surfaced without depleting their oxygen content for effective foraging and locomotion. These dichotomous dive tactics were apparently the result of behavioral modifications by turtles depending on the aim of each dive. The dichotomy in the respiratory patterns at the surface may allow researchers to estimate the activity state of sea turtles during boat-based and aerial surveys.

**References**


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