

Difference in Flipper Beating Frequency of Green Turtles in Water and on Land

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ABSTRACT

Sea turtles spend most of their lives in marine habitats, but they require a terrestrial environment for oviposition. In both conditions, they use limbs for thrust production. We attached animal-borne data loggers on green turtle and calculated the stroke frequency during swimming in water and crawling on land from surging acceleration. Stroke frequency was compared during swimming and crawling. The results showed that stroke frequency during terrestrial crawling is significantly higher than during swimming. This contrasts with previous studies of animals performing drag-based swimming. Because green turtles are considered to be lift-based swimmers that produce thrust mainly by dorsoventral excursion, one hypothesis is that anteroposterior excursion may be restricted despite its importance in terrestrial crawling and drag-based swimming. Small anteroposterior excursion resulting in short stride length may be complemented by higher stroke frequency during crawling.

KEYWORDS: *Chelonia mydas*, stroke, aquatic, terrestrial

INTRODUCTION

Many organisms undergo transitions between aquatic and terrestrial environments, presenting a drastic change in the animal's physical conditions (Denny, 1990). Such organisms employ somewhat similar, yet different locomotion patterns of the same thrust organs during aquatic and terrestrial locomotion (Rivera and Blob, 2010; Pace and Gibb, 2011). For vertebrates using limbs to propel themselves, the limb cycle is an important property for understanding the pattern of thrust production both in water and on land.

In previous studies of amphibious animals performing drag-based swimming, such as freshwater turtles *Trachemys scripta* (Gillis and Blob, 2001; Rivera and Blob, 2010), mudskippers *Periophthalmus argentilineatus* (Pace and Gibb, 2009), mallard ducks *Anas platyrhynchos* (Biewener and Corning, 2001), and opossum *Lutreolina crassicaudata* (Santori et al., 2005), limb cycle frequency was reported to be higher during aquatic than terrestrial locomotion or similar in both types of locomotion. The contrasts between aquatic and terrestrial locomotor movements may be passive consequences of interactions with disparate physical environments of water and land, but many kinematic changes between water and land are correlated with changes in motor and strain patterns, suggesting that they are controlled actively for moving effectively through both aquatic and terrestrial environments (Gillis and Blob, 2001).

However, comparison of the limb cycle of animals performing effective lift-based swimming between in-water and on-land has been less studied. For lift-based swimming, dorsoventral excursion mainly produces thrust, whereas anteroposterior excursion of limbs contributes to thrust production for drag-based swimming and terrestrial walking (Alexander, 1989, 2003). Therefore, if lift-based swimmers have some restrictions on anteroposterior excursion for aquatic adaptation, their terrestrial locomotion will be constrained.

Here we focus on one of the sea turtle species, green turtle, *Chelonia mydas*, that is known to use a similar gait under both conditions, synchronous movement of foreflippers, and performing lift-based swimming for adaptation to effective long-term migratory swimming (Davenport et al., 1984; Wyneken, 1997; Renous et al., 2000). Flipper beat frequency between in-water and on-land situations was compared.

MATERIALS AND METHODS

We performed nightly patrols of the beach at Ishigaki Island of Japan in July and August of 2008 and 2009. When we found turtles on the beach, to minimize disturbance, we stayed away at the coastline until they began laying eggs or returning to the sea. When they returned to the sea, we attached or removed W1000L-3MPD3GT data loggers (26 mm in diameter, 175 mm in length, 135 g in air; Little Leonardo Co., Ltd. Japan) four times in total, on the carapace of three female green turtles (straight carapace length: 96.0, 97.6, and 101.1 cm; ID in Table 1). Because green turtles nest several times in one season, when turtles attached with loggers went to the sea and returned to nest later, data loggers were removed.

The logger was set to record tri-axial accelerations at 16 Hz (ID2) or 8 Hz (ID1, ID3a, and ID3b). In addition, depth, swim speed, temperature, and tri-axial geomagnetism were recorded at 1 s intervals for all implementations. Data loggers started recording after 48 h from the setting for one implementation (ID2) and immediately after the setting for three implementations (ID1, ID3a, and ID3b).

Data was downloaded to a computer and analyzed using Ethographer (Sakamoto et al., 2009) with the software IGOR Pro (WaveMetrics Inc., USA). Acceleration sensors were calibrated to m s^{-2} by rotating devices through known angles in all three spatial planes. Dynamic (i.e. owing to flippers' thrust) of surge acceleration measured by data loggers were extracted using the continuous wavelet transformation (CWT) filter at minimum cycle of 0.25 s and maximum cycle of 10 s because motions of sea turtles at higher than 4 Hz were negligible. Static acceleration (i.e. related to animal posture) as lower frequency residual was used to calculate the pitch angle of animals.

Whether turtles were in water or on land was determined from the depth data. When turtles swam in water, the periods with differential of pitch angle $< -3^\circ$ and depth < 1 m were estimated as breathing, and the duration between them was defined as a swimming duration. Swimming durations during which continuous flipper beating (i.e. continuous peaks of dynamic acceleration and swim speed > 0) was recorded, and were selected from the periods when turtles swam continuously in the shallow water ('Type 5' dives in Houghton et al. (2002)) with probably little effect of buoyancy, before and after landing on the beach. Stroke frequency was calculated as inverse of time interval between peaks of dynamic surging acceleration. When turtles crawled on land, the periods with an absolute value of dynamic acceleration $\geq 0.3 \text{ m s}^{-2}$ within 3 s were defined as crawling duration. Stroke frequency was calculated as inverse of time interval between peaks $\geq 0.5 \text{ m s}^{-2}$ of dynamic surging acceleration, but peaks $\geq 0.5 \text{ m s}^{-2}$ within 1 s were defined as one peak. Stroke frequency was averaged over each swimming or crawling duration. We compared the difference in stroke frequency by generalized linear model followed by analysis of deviance. In the model, the stroke frequency was modeled as the response variable using a gamma distribution with a log link function. The difference between swimming in water and crawling on land was coded as an explanatory variable. In addition, the effect of attaching the data logger, which reflects individual difference or attachment site differences (ID in Table 1), was included as an explanatory variable.

Table 1 Summary of number of durations and average (\pm SD) of duration, number of strokes, and stroke frequency during aquatic swimming and terrestrial crawling. Data acquired 2 times from the same individual were denoted by ID 3a and 3b.

ID	no. of durations		duration (s)		no. of strokes		stroke frequency (Hz)	
	swim	crawl	swim	crawl	swim	crawl	swim	crawl
1	139	32	135.3 (± 112.5)	12.2 (± 4.9)	36.0 (± 28.2)	4.5 (± 1.5)	0.284 (± 0.055)	0.342 (± 0.041)
2	253	49	199.3 (± 124.9)	16.7 (± 9.5)	49.1 (± 29.2)	6.8 (± 3.6)	0.257 (± 0.047)	0.378 (± 0.043)
3a	233	40	123.0 (± 82.8)	14.2 (± 6.1)	36.9 (± 25.7)	6.0 (± 2.0)	0.313 (± 0.063)	0.397 (± 0.035)
3b	119	26	110.2 (± 88.0)	15.1 (± 5.2)	36.9 (± 30.5)	6.7 (± 2.1)	0.353 (± 0.072)	0.415 (± 0.026)

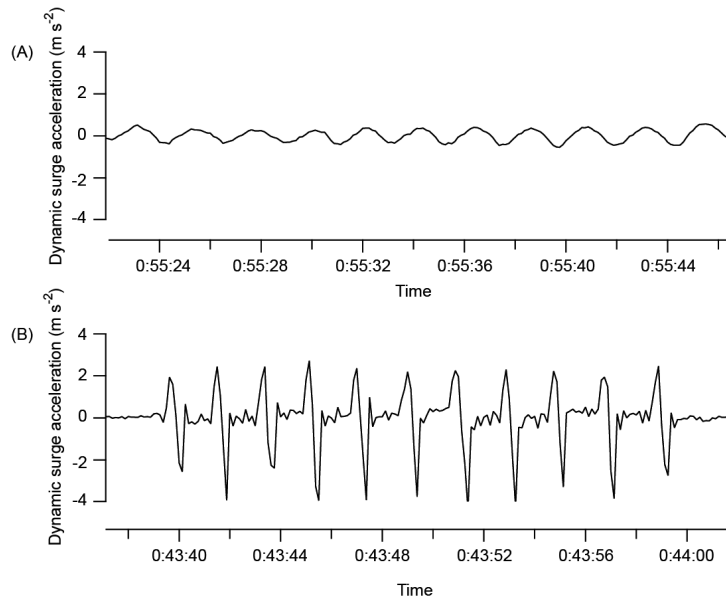


Fig. 1 Typical dynamic surge acceleration during (A) swimming and (B) crawling.

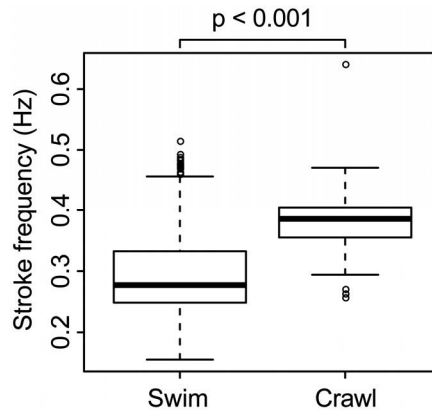


Fig. 2 Boxplot of stroke frequency in water and on land.

RESULTS

A total of 744 swimming and 147 crawling durations were analyzed (Fig. 1). Average (\pm SD) swimming and crawling durations, number of strokes per duration, and stroke frequency of each ID are listed in Table 1. The results of analysis of deviance show that the type of locomotion, swimming or crawling, had significant effect on stroke frequency ($p < 0.001$), in addition to the difference in ID. That is, stroke frequency during terrestrial crawling is significantly higher than that during swimming (Fig. 2).

DISCUSSION

In this study, we analyzed the shallow continuous swimming considered to be traveling (Houghton et al., 2002) and crawling on land for depositing eggs (Hailman and Elowson, 1992), both of which employ vigorous activity. Outliers detected during swimming were larger than crawling frequency, which may reflect that some types of swimming activity were included. Nevertheless, this study showed that green turtles mostly employed higher stroke frequency on land than in water. This is in contrast to the fact that higher stroke frequency is limited during crawling on sand because of the slipping and reduced efficiency of locomotion (Mazouchova et al., 2010). The result also contrasts with previous studies of animals performing drag-based swimming (Biewener and Corning, 2001; Gillis and Blob, 2001; Santori et al., 2005; Pace and Gibb, 2009; Rivera and Blob, 2010).

Among sea turtles, loggerhead turtles, *Caretta caretta*, are known to employ large dorsoventral excursions but small anteroposterior excursions during swimming, although freshwater turtles of drag-based swimmers, *Trachemys scripta*, employ large anteroposterior excursions (Rivera et al., 2011). Although several factors may have impact on the difference (e.g. terrestrial locomotion during nesting is more vigorous than traveling in water), one hypothesis is that lift-based swimmers such as sea turtles have so adapted to efficient swimming that anteroposterior excursions are restricted. Small anteroposterior excursion resulting in short stride length is considered to be complemented by higher stroke frequency during crawling.

ACKNOWLEDGEMENTS

The fieldwork was assisted by the following people: the members of the Ishigaki Island Sea Turtle Research Group; the staff of the Research Center for Subtropical Fisheries; D. Imakita (Kinki University); Y. Kawabata, K. Ichikawa, H. Watanabe, T. Hashiguchi, T. Koizumi, and A. Nakabayashi (Kyoto University). This study was partly supported by the Global COE Program, Informatics Education and Research for a Knowledge-Circulating Society.

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