



Do loggerhead turtle (*Caretta caretta*) eggs vary with alternative foraging tactics?

Hideo Hatase^{a,*}, Kazuyoshi Omuta^b, Teruhisa Komatsu^a

^a Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan

^b Yakushima Sea Turtle Research Group, 489-8 Nagata, Yakushima, Kagoshima 891-4201, Japan



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ABSTRACT

Quantifying variations in the size and viability of offspring is essential to accurately evaluate fitness differences between alternative life histories. In the present study, the size and nutritional components (water, protein, lipid, carbohydrates, and ash) of loggerhead turtle (*Caretta caretta*) eggs were compared between small planktivores inhabiting oceanic areas (water depths >200 m) and large benthivores inhabiting neritic areas (depths <200 m) that sympatrically nest on Yakushima Island, Japan. We aimed to verify whether variations in the diet, which are dependent on the environment, of a large marine reptile influence egg quality. No significant differences were found in the size or component values of eggs between oceanic and neritic foragers classified based on stable isotope ratios in the yolks. The above results imply that foraging tactics adopted by loggerhead turtles do not affect the characteristics of the eggs and hatchlings. Among all 20 nesting females analyzed, egg mass increased significantly with straight carapace length, and the absolute contents for all components (except carbohydrates) significantly increased with egg mass. Interspecies and intrapopulation variations in egg characteristics are discussed in relation to adaptations to local environments.

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1. Introduction

Reproductive resources are finite; therefore, their allocation to reproductive traits such as egg size, egg number, and frequency of oviposition can lead to trade-offs among such traits (Smith and Fretwell, 1974). An increase in egg size may lead to a decrease in egg number, while enhanced oviposition frequency may reduce individual egg size as well as egg number. The allocation patterns of reproductive resources to each trait exhibited by species are optimized to maximize their fitness through natural selection. Even within the same gene pool, the way of resource allocation can be modified in response to environmental conditions (via phenotypic plasticity). For example, in several aquatic animals, females that experienced food constraints displayed plasticity in resource allocation by producing fewer but larger eggs or heavier offspring (Iguchi, 2012; Jonsson et al., 1996; Reznick and Yang, 1993).

Sea turtles are long-lived, iteroparous animals that lay several clutches of numerous eggs (ca. 100 eggs per clutch) during a single nesting season on specific sandy beaches, and remigrate there from distant feeding grounds every few years (Hamann et al., 2003; Van Buskirk and Crowder, 1994). Trade-offs among the reproductive traits of sea turtles, especially between egg size and clutch size (number of eggs per clutch), have been a topic of interest among sea turtle research communities (Bjorndal and Carr, 1989; Hays and Speakman, 1991; Tiwari

and Bjorndal, 2000; Van Buskirk and Crowder, 1994; Wallace et al., 2007). To date, although there are variations in both egg size and clutch size within sea turtle populations, the trade-off between egg size and clutch size has not been recognized at the intrapopulation level; however, it has been recognized at the interpopulation or interspecies level. In recent years, owing to the prevalence of satellite telemetry and stable isotope analysis, intrapopulation variation in the use of foraging habitats by sea turtles has attracted broad interest (e.g., Ceriani et al., 2012; Hatase et al., 2002, 2006; Hawkes et al., 2006; Mansfield et al., 2009; McClellan et al., 2010; Pajuelo et al., 2012; Rees et al., 2012; Seminoff et al., 2008). Behavioral variations in sea turtles are tightly coupled with variations in several life history traits such as body size, age at reproduction, clutch size, clutch frequency (number of clutches per season), breeding frequency (number of nesting seasons), and remigration intervals (the intervals between successive nesting years) (e.g., Caut et al., 2008; Eder et al., 2012; Hatase et al., 2013; Vander Zanden et al., 2014; Zbinden et al., 2011), which raised a question whether well-known egg size variation within sea turtle populations may also be attributed to variation in their use of foraging habitats.

Among loggerhead turtles (*Caretta caretta*) nesting on a Japanese beach, large females that forage mainly on benthic animals in neritic areas (water depths <200 m) laid larger and more numerous clutches by remigrating more frequently at shorter intervals than small females that forage mainly on macroplankton in oceanic areas (depths >200 m), resulting in a 2.4-fold difference in the reproductive output (Hatase et al., 2013). This suggests that neritic foragers have a higher level of

* Corresponding author. Tel.: +81 4 7136 6228; fax: +81 4 7136 6227.
E-mail address: hatase@aori.u-tokyo.ac.jp (H. Hatase).

fitness than oceanic foragers. To accurately evaluate the fitness differences between foraging tactics, however, it is essential to investigate the trade-off between the quantity and quality of offspring. That is, if the survival rate of offspring from oceanic foragers during the period from aboveground emergence to first reproduction were 2.4 times higher than that from neritic foragers, then this would offset the 2.4-fold greater productivity of neritic foragers; thus, the fitness of the two foraging tactics might be similar. We would then reconsider the mechanism that maintains alternative life histories in a loggerhead turtle population, which was considered to be a conditional strategy (Hatase et al., 2013). Theoretically, offspring size is positively correlated with survival (Parker and Begon, 1986; Smith and Fretwell, 1974). In fact, larger hatchlings of a freshwater turtle showed a greater survival rate (Janzen, 1993), although differential survival at the egg and hatchling stage may not last to later stages among long lived sea turtles (Heppell et al., 2003). Hatchling size is likely to increase with egg size within and among several sea turtle populations (Özdemir et al., 2007; Pinckney, 1990; Van Buskirk and Crowder, 1994; Wallace et al., 2006b, 2007).

In the present study, egg size was compared between oceanic and neritic foragers of the loggerhead turtle, which were classified based on stable isotope ratios in the yolks. The nutritional components of the eggs were also compared between the two foraging tactics because they may affect body size and the survival of offspring. For example, lipid or dry matter content has been closely related to post-hatching energetic demands in freshwater turtles (Congdon and Gibbons, 1985; Finkler et al., 2004). On the basis of the results of our analyses, we verified whether variations in diet (dependent on the environment) for a large marine reptile affect egg characteristics. Furthermore, we discussed interspecies and interpopulation variations in egg characteristics in relation to adaptations to local environments.

2. Materials and methods

2.1. Surveys of nesting females and egg collection

Nightly patrols looking for nesting turtles were conducted on foot at the adjacent beaches of Inakahama (1.0 km in length) and Maehama (0.9 km) (30°24'N, 130°26'E), Nagata, Yakushima Island, Kagoshima Prefecture, Japan, from May 15 to 24, 2013. At this study site, tagging surveys of nesting turtles have been ongoing by the Yakushima Sea Turtle Research Group annually since 1985 (Hatase et al., 2013). Individual female loggerheads were identified by external plastic tags (MultiFlex P, Caisley, Bocholt, Germany), placed on both the front and rear flippers, and an internal tag (ID-100, Trovan, East Yorkshire, UK), inserted into the left front flipper; alternatively, previously existing tags were used for identification. The straight carapace lengths and widths of nesting females were measured with calipers during oviposition. We selected 10 small females with a straight carapace length and width of <800 mm and <630 mm, respectively, and 10 large females with a straight carapace length and width of ≥800 mm and ≥630 mm. Because the loggerhead turtle is an endangered species, we set the sample size of eggs as small as possible. Eggs laid by 20 females, in total, were sampled for analyses of nutritional components and stable isotopes. Five eggs per clutch of each individual female were randomly collected during oviposition and maintained at −20 °C until analytical preparation. One hundred eggs were thawed, and their size and mass were examined. Egg size was measured as the maximum diameter to the nearest 0.1 mm using vernier calipers. Egg mass was weighed to the nearest 0.01 g using a digital scale. Four eggs out of five eggs collected from each female were used for analysis of nutritional components, while one remaining egg was used for stable isotope analysis.

2.2. Analysis of the nutritional components in eggs

In a loggerhead turtle, 98.15% of the albumen is water (Yamauchi et al., 1984). Therefore, we did not separate the albumen from the

yolk. The yolks and albumens of four eggs from each female were combined and weighed. Shell wet mass was calculated by subtracting the mass of the combined yolks and albumens from the sum of the four egg masses and dividing the resultant value by four. The water content of the combined yolks and albumens was determined gravimetrically by the mass change in a sample after drying in a vacuum oven at 100 °C for 5 h. The dry matter included ash, lipids, protein, and carbohydrates. Ash, lipid, and protein analyses were performed on subsamples of the dry yolks and albumens. The ash content was determined gravimetrically by the mass change in a subsample after combustion in a furnace at 550 °C for 6 h. The lipid content was determined gravimetrically by chloroform–methanol extraction. The protein content was estimated from the total nitrogen content, which was determined using the Kjeldahl method and a conversion factor of 6.25 (Yasumoto et al., 2006). The carbohydrate content was calculated by subtracting the content values for water, ash, lipids, and protein from 100 g of the wet yolks and albumens. The absolute content of each component per yolk and albumen (per shell-free egg) was calculated from the percentage of each component, as determined by the combined values for the four yolks and albumens. The energy content was estimated based on physical heat of combustion of 5.7 kcal g^{−1} for protein, 9.4 kcal g^{−1} for lipid, and 4.1 kcal g^{−1} for carbohydrates, with 1 kcal being equal to 4.184 kJ (Yasumoto et al., 2006).

2.3. Measurements of the stable isotope ratios in the yolks and classification into foraging-habitat groups

Stable carbon and nitrogen isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in the yolks were measured following the methods described by Hatase et al. (2002, 2006). $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were expressed as deviations from the standard, as defined by the following equation:

$$\delta^{13}\text{C} \text{ or } \delta^{15}\text{N} = \left(R_{\text{sample}} / R_{\text{standard}} - 1 \right) \times 1000 (\text{‰})$$

where R is $^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$. Pee Dee Belemnite (PDB) and atmospheric nitrogen were used as the carbon and nitrogen isotope standards, respectively. Analytical precision was $\leq 0.19\text{‰}$ for $\delta^{13}\text{C}$ and $\leq 0.29\text{‰}$ for $\delta^{15}\text{N}$. Following the findings of a previous study that simultaneously conducted stable isotope analysis and satellite telemetry on the same females (Hatase et al., 2002), females producing yolks with a $\delta^{13}\text{C}$ of less than −18.0‰ and a $\delta^{15}\text{N}$ of <12.0‰ were grouped as oceanic planktivores, and females with a $\delta^{13}\text{C}$ of greater than or equal to −18.0‰ or a $\delta^{15}\text{N}$ of $\geq 12.0\text{‰}$ were grouped as neritic benthivores (Hatase et al., 2013). The complete data set, including $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the yolks, body size, and egg size and components for individual loggerhead turtles, is available as electronic supplementary material (Appendix A).

3. Results

Female loggerheads were divided into two groups based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the egg yolks (Fig. 1). There were nine oceanic planktivores and 11 neritic benthivores. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the oceanic foragers ranged from −20.5 to −18.6‰ and 8.9 to 11.4‰, respectively, while those of neritic foragers ranged from −19.1 to −17.0‰ and 12.0 to 13.7‰.

There were significant differences in the straight carapace length and width between the oceanic and neritic foragers (*t*-test: $p < 0.05$ and < 0.05 , respectively; Table 1). Oceanic foragers had shorter and smaller mean straight carapace lengths and widths, respectively, than those of the neritic foragers. There were minimal variations in egg size and mass within clutches, and the differences in their coefficients of variation (CVs) between the two foraging groups were not significant (*t*-test: $p = 0.86$ and 0.17 , respectively; Table 1). The mean size and mass among five eggs from each female were used for the following

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