BASAL METABOLIC RATE OF THE RHINOCEROS AUKLET
CERORHINCA MONOCERATA, AS MEASURED USING RESPIROMETRY

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Basal metabolic rate (BMR) is the energy required by an animal when at rest, assuming thermoneutrality and no metabolic work for digestion (Schmidt-Nielsen 1997). BMR has been used to calculate an index of metabolic intensity and of the magnitude of energy expenditure, which is the ratio of field metabolic rate to BMR (Fyhn *et al*. 2001, Ellis & Gabrielsen 2002). BMR in seabirds differs depending on several ecological traits such as flight activity, migration and breeding stage (Bech *et al*. 1999, 2002, McNab 2009), as well as physiological states such as size of body components (Daan *et al*. 1990) and the climate and latitude of their habitat (Ellis 1984). Therefore, measuring the BMR for individual species is important for understanding seabird energetics.

Rhinoceros Auklets *Cerorhinca monocerata* are medium-sized alcids that breed in temperate waters in the northern Pacific (Gaston & Jones 1998). Similar to other alcids (e.g., Elliott *et al*. 2010, Ito *et al*. 2010), Rhinoceros Auklets are pursuit divers capable of dives of up to 60 m deep (Kuroki *et al*. 2003, Watanuki *et al*. 2006). Because diving birds tend to have higher BMR than non-diving birds (Ellis 1984, Bryant & Furness 1995) and because birds that breed in temperate and polar regions have higher BMR than those breeding in tropical regions (McNab 2009), the auklets are expected to have a relatively high BMR. However, no studies to date have measured BMR in Rhinoceros Auklets. Thus, the present study provides the first description of BMR in Rhinoceros Auklets.

Our experiment was conducted at Teuri Island (44°25′N, 141°19′E), Hokkaido, Japan, from 21 June to 3 July 2010. All experiments were performed according to a protocol approved by the Institutional Animal Care and Use Committee of Nagoya University. To measure metabolic rate using respirometry, five Rhinoceros Auklets were captured at night at a breeding colony. The birds were held in darkened boxes, transported to the laboratory within 10 min and kept for at least one hour to minimize the effects of capture stress on the metabolic rate. The body mass of each bird was measured to the nearest 5 g using a Pesola spring balance, and the birds were placed in a metabolic chamber. They were removed from the chamber 24 h later, immediately weighed again, and released at the colony. A linear decrease in body mass was assumed when assessing the body mass value used for calculating the mass-specific metabolic rate.

Oxygen consumption rate (V_{O2}) was measured using an open-flow respirometric system composed of a 20-L acrylic metabolic chamber (20 cm long × 25 cm high × 40 cm wide) and an oxygen analyzer (Xentra 4100, Servomex Ltd; Shirai *et al*. 2012a, b). The accuracy of the oxygen analyzer was better than 0.02% over the entire (0%–100%) range of oxygen levels. The metabolic chamber was submerged in a thermostatic water bath and maintained at 22.3 ± 1.5°C (SD), which was assumed to be within the thermoneutral zone of this species. Based on an equation from Ellis and Gabrielsen (2002), we assumed the lower end of their thermoneutral zone (i.e., the lower critical temperature) to be 15°C. The chamber temperature (Tc) was recorded using a temperature sensor (± 0.7°C, Thermocron Type-SL, KN Laboratories, Inc.) at 1 min intervals. Atmospheric pressure (Pa) was measured using a data logger (± 1.5 hPa, TR-73U Thermo Recorder, T&D Corp.) at 1 min intervals, and the mean value during our experiment was 1006.3 hPa (± 1.7 SD). The flow rate (V_E) of the chamber was fixed at 2.0 L · min^{-1} using a mass flow controller (± 2%, TYPE HM1171A, TOKYO KEISO CO., LTD). Effluent air was dried over silica gel, and a fraction of the dry effluent air was directed into the oxygen analyzer. The oxygen analyzer was calibrated using dry outside air (set at 20.946% oxygen) and pure stock nitrogen (set to 0.000% oxygen). Oxygen concentrations in effluent air (F_{EO2}) were read by a computer every minute. Values of V_{O2} were calculated using formula 3A in Withers (1977) as follows,

$$V_{O2} = \frac{V_E \times (F_{IO2} - F_{EO2})}{1 - (1 - RQ) \times F_{IO2}} .$$

We assumed a respiratory quotient (RQ) of 0.8, which minimizes error in the estimated rate of energy expenditure when RQ is unknown (Koteja 1996), and an oxygen concentration of influent air (F_{IO2}) of 20.946%. In calculating energy expenditure from V_{O2}, a conversion coefficient of 20.1 kJ · L^{-1} was used (Schmidt-Nielsen 1997). All results are given at standard temperature and pressure and dry (STPD).

In general, BMR is defined as the lowest level of V_{O2} with arbitrary intervals. However, since metabolic rate, even during resting, may be affected by slight changes in body temperature, hormone levels and a host of other underlying physiological processes, shorter calculation intervals may lead to high stochastic variance (Hayes *et al*. 1992). On the other hand, longer calculation intervals may include periods of activity (Hayes *et al*. 1992). As in other studies (e.g., Bech *et al*. 1999, Fyhn *et al*. 2001), we calculated the minimal metabolic rate of the auklets with various intervals, ranging from 2 to 60 min, based on the procedure of Meerlo *et al*. (1997). All values presented are means ± SD.

The mean minimal metabolic rate increased continuously with interval length, but the rate of increase changed at an interval of about 20 min (Fig.1). Consequently, we assumed that a 20 min interval would minimize the effects on minimal metabolic rate of both the underlying physiological processes and the period of activity, so we estimated BMR as the minimal level of metabolic rate over an interval of 20 min.

The mean BMR of the five Rhinoceros Auklets (mean body mass 524 ± 39 g) was 0.0248 ± 0.0042 kJ · g^{-1} · h^{-1}. This result is 153% of the predicted BMR using a body mass of 524 g from McNab's (2009) equation for birds as follows:

$$BMR(kJ \cdot h^{-1}) = 0.145m^{0.652}$$

where *m* is body mass in grams.

Other Alcidae (Common *Uria aalge* and Thick-billed Murres *U. lomvia*, Little *Alle alle* and Razor-billed Auks *Alca torda*, Atlantic Puffins *Fratercula arctica*, and Black Guillemot *Cepphus grylle*) also exhibit 40%–105% higher measured BMRs than values predicted using the equation for all birds (summarized body masses and measured BMR in McNab [2009]). Together, these results indicate that Alcidae have higher BMRs than other birds of similar size. This relatively higher BMR of Rhinoceros Auklets may be related to their diving habit as well as to the climate and latitude of their habitat (Ellis 1984, Bryant & Furness 1995, Ellis & Gabrielsen 2002, McNab 2009).

In birds, the sizes of metabolically active organs such as the heart and kidney are a major determinant of BMR (Daan *et al*. 1990). In general, a large heart mass may contribute to diving efficiency during a foraging trip because it enables an increase in lung perfusion, reducing recovery time between dives (Drabek & Tremblay 2000). Birds with salt glands have larger kidneys than birds without them because the former need to reabsorb sodium for concentrated salt gland secretion (Hughes 2003). Because the mean heart and kidney masses of Rhinoceros Auklets rearing chicks (Niizuma *et al*. 2002) were 104% and 138% of predicted values from allometric equations of heart (Grubb 1983) and kidney mass (Johnson 1968) for birds, respectively, these body components might contribute to the relatively higher BMR in Rhinoceros Auklets.

Birds that breed at higher latitudes (in temperate and polar regions) generally have higher BMRs than those that breed at lower latitudes (in tropical regions) (Ellis 1984, McNab 2009). In colder environments, selection might be expected to favor individuals with a greater capacity for thermoregulation, requiring more energy
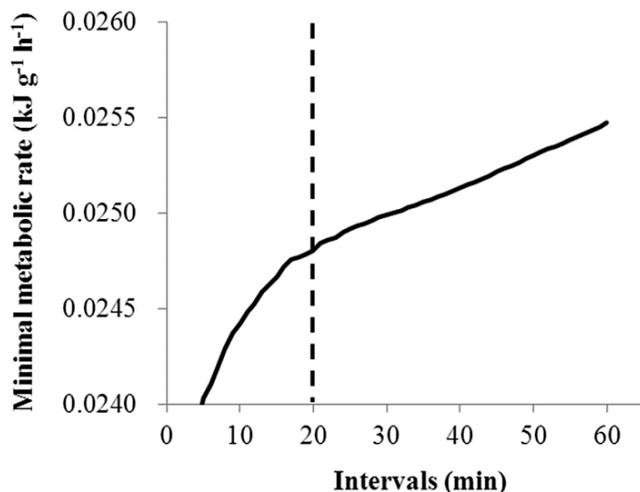
intake and larger organs to process food (e.g., Kersten *et al*. 1998, Wiersma *et al*. 2012). Because most Alcidae breed in temperate to polar regions (Vermeer *et al*. 1987), these climatic factors might influence the high BMR in Rhinoceros Auklets and other Alcidae.

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Fig. 1. Mean minimal metabolic rate (kJ · g^{-1} · h^{-1}) of five Rhinoceros Auklets in relation to the length of the interval used for calculation. In the present study, BMR was defined as the lowest level of metabolic rate over a 20 min interval.

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