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Resting metabolic rate and heat increment of feeding in juvenile South American fur seals (*Arctocephalus australis*)

M. Dassis [a,b,*], D.H. Rodríguez [a,b], E.N. Ieno [c], P.E. Denuncio [a,b], J. Loureiro [d], R.W. Davis [e]

[a] Instituto de Investigaciones Marinas y Costeras, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Mar del Plata, CONICET, Funes 3350, 7600 Mar del Plata, Argentina
[b] Consejo Nacional de Investigaciones Científicas y Técnicas, Rivadavia 1917, PB, C1033AAJ Ciudad Autónoma de Buenos Aires, Argentina
[c] Highland Statistics Ltd., P.O. Box 82, Av. Escandinavia 72, 03130, Spain
[d] Fundación Mundo Marino, Avenida Décima N° 157, 6-7105 San Clemente del Tuyú, Argentina
[e] Department of Marine Biology, Texas A&M University at Galveston, 200 Seawolf Parkway, Ocean and Coastal Studies Building, Galveston, TX 77553, USA

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ABSTRACT

Bio-energetic models used to characterize an animal's energy budget require the accurate estimate of different variables such as the resting metabolic rate (RMR) and the heat increment of feeding (HIF). In this study, we estimated the in air RMR of wild juvenile South American fur seals (SAFS; *Arctocephalus australis*) temporarily held in captivity by measuring oxygen consumption while at rest in a postabsorptive condition. HIF, which is an increase in metabolic rate associated with digestion, assimilation and nutrient interconversion, was estimated as the difference in resting metabolic rate between the postabsorptive condition and the first 3.5 h postprandial. As data were hierarchically structured, linear mixed effect models were used to compare RMR measures under both physiological conditions. Results indicated a significant increase (61%) for the postprandial RMR compared to the postabsorptive condition, estimated at 17.93 ± 1.84 and 11.15 ± 1.91 mL O_2 min^{-1} kg^{-1}, respectively. These values constitute the first estimation of RMR and HIF in this species, and should be considered in the energy budgets for juvenile SAFS foraging at-sea.

1. Introduction

The field of bioenergetics focuses on the partitioning of energy by organisms (Enders and Scruton, 2006). The basic principle of bioenergetics is that all energy acquired through food ingestion is deposited as new body tissue, used in metabolic processes or ultimately lost as waste in feces and excretion. Therefore, bioenergetics provides a method to quantitatively assess an animal's effort in acquiring resources and the way in which these resources are allocated (Costa, 2008) and constitutes a framework for the study of relationships between organisms and different environmental conditions (Enders and Scruton, 2006). Bioenergetic models developed for marine mammals have ranged from simple equations representing average energy expenditure to detailed energy budgets for each age, sex-class and season based on both laboratory and field measurements (Hinga, 1979; Naumov and Chekunova, 1980; Ashwell-Erickson and Elsner, 1981; Doidge and Croxall, 1985; Hiby and Harwood, 1985; Lavigne et al., 1985; Worthy, 1987; Øritsland and Markussen, 1990; Härkönen and Heide-Jørgensen, 1991; Markussen and Øritsland, 1991; Ryg and Øritsland, 1991; Markussen et al., 1992; Olesiuk, 1993; Ugland et al., 1993; Mohn and Bowen, 1996; Bowen, 1997; Stenson et al., 1997; Winship et al., 2002). The reliability of predictions of bioenergetics models is strongly dependent on the accuracy of the input variables (Enders and Scruton, 2006). An important variable in these models is the resting metabolic rate (RMR); or the rate of energy consumption by an animal while at rest. The difficulty in measuring RMR in marine mammals has confused inter-species comparisons as many studies did not conform to standardized criteria for measurements that include adult age, resting, thermally neutral, and post-absorptive (Lavigne et al., 1986).

Another variable included in bio-energetic models is the heat increment of feeding (HIF) [also called specific dynamic action (SDA) or diet-induced thermogenesis], which is the increase in metabolic rate associated with ingestion of a meal (Rubner, 1902; Maynard and Loosli, 1969). Understanding the physiological causality of this phenomenon has a long history in comparative nutritional and physiological research and includes a multitude of preabsorptive, absorptive and postabsorptive processes (McCue, 2006). HIF can be expressed as a function of the absolute mass of food ingested (Lusk, 1912–1913a; 1912–1913b; 1915; Wilhelmj and Bollman, 1928; Wilhelmj et al., 1931), as a function of the caloric value of the meal (Lusk, 1910; 1922; Kriss et al., 1934; Kriss, 1938; Kriss and Marcy, 1940), as a function of the relative mass of each prey species (Muir and Niimi, 1972; Janes and Chappell, 1995;

Abbreviations: BMR, basal metabolic rate; HIF, heat increment of feeding; RMR, resting metabolic rate; SAFS, South American fur seals.

* Corresponding author at: Casilla de Correos 1260 Correo Central (7600) Mar del Plata, Argentina.
E-mail address: marieladassis@gmail.com (M. Dassis).

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Secor and Phillips, 1997; Hopkins et al., 1999; Overgaard et al., 1999; Busk et al., 2000; Hicks et al., 2000; Secor, 2003; Roe et al., 2004), as a function of the percent of protein in the meal (Hamada and Maeda, 1983; Chakraborty et al., 1992) or as the difference between post-absorptive and postprandial metabolic rates (MacArthur and Campbell, 1994; Chappell et al., 1997; Rosen and Trites, 1997; Nespolo et al., 2003; Rosen and Trites, 2003; Bech and Praesteng, 2004; Enstipp et al., 2008). The variety of methods reflects the complexity of this process and the need for measurements that contribute to estimates of overall energetic budgets.

The South American fur seal (SAFS, *Arctocephalus australis*, Zimmermann 1783) is a relatively small species of pinniped with an insular distribution that extends along the coast of South America, from Southern Brazil to Central Perú (Vaz-Ferreira, 1982). The main breeding area of this species in the Atlantic Ocean includes six colonies on islands off the coast of Uruguay (Vaz-Ferreira, 1982; Vaz-Ferreira and Ponce de León, 1987; Bastida and Rodríguez, 2003; Ponce de León and Pin, 2006). Although many aspects of the life history and ecology of this species have been studied, there have been no previous measurements of RMR or HIF.

The goals of this study were to measure the in air RMR in male SAFS and to estimate HIF through comparisons of postabsorptive and postprandial RMR. The study was performed on juvenile animals, for which these energetic parameters are even more critical to foraging success, and focused on the first 3.5 h after feeding.

2. Materials and methods

2.1. Animals and measurement of RMR in air

The in air RMR was estimated by measuring oxygen consumption in five juvenile (mean body mass 13.2 ± 1.3 kg) male SAFS under postabsorptive conditions (16 h since last feeding) at the Mundo Marino Aquarium (San Clemente de Tuyú, Argentina) from March to April 2007. These animals originally stranded on beaches close to the aquarium and were rehabilitated during a 3–5 month period. Prior to metabolic measurements, all animals were judged by the veterinarians to be healthy and ready for release.

Animals were placed in a metabolic box (1.2 m long, 0.8 m wide, 0.8 m high) connected to an open flow respirometry system (Sable System International, Inc., Henderson, NV, USA). Air was drawn through the metabolic box with a Sable Systems Mass Flow pump at an adjustable flow rate that ranged from 200 to 250 l min^{-1}. At these flows, the percentage of oxygen in the box remained above 20%. A continuous subsample of air from the exhaust port was dried (Drierite) and scrubbed of carbon dioxide (Sodasorb) before entering an FC-1 oxygen analyzer. The percentage of oxygen in the expired air was monitored continuously and recorded once per second using the Sable Systems ExpeData software. Oxygen consumption ($\dot{V}o_2$, mL O_2 min^{-1} kg^{-1}) was calculated using equations from Depocas and Hart (1957) and calibrated in triplicate according to Davis et al. (1985). A respiratory quotient of 0.77 was assumed according to measurements (the amount of CO_2 produced per unit of O_2 consumed) performed in Antarctic fur seals *Arctocephalus gazella* (Arnould et al., 2001). During calibration, oxygen concentrations in the metabolic box were 99.29 ± 0.04% and 99.52 ± 0.02% of the predicted values for N_2 flows of 2 l min^{-1} and 5 l min^{-1}, respectively.

Fur seals were kept in the metabolic box for 2–3 h while oxygen consumption was continuously measured. These experimental runs were performed once per day with each animal starting at the same time (10:00 am) to prevent possible diel fluctuations in basal metabolic rate from affecting measurements. To avoid an increase in metabolism associated with occasional movement of the animals within the box, resting metabolic rate ($\dot{V}o_2$) was determined during periods of at least 10 min (range = 10–24) of continuous resting behavior (lying motionless and awake) and a steady rate of oxygen consumption. The number of $\dot{V}o_2$ measurements per experimental run (range = 2–7) differed among animals depending on their behavior.

The average air temperature inside the box during measurements (18.3 ± 2.4 °C; range = 14–20) was included within the thermal neutral zone (TNZ) of Northern fur seals (*Callorhinus ursinus*) resting in water (8.3–24.3 °C; Liwanag, 2010), which allowed us to assume thermo neutrality in our experiments. In addition, no thermoregulatory behavior (flipper movements and/or hyperventilation) was observed during measurements. All measurements followed standard criteria for measuring basal metabolic rate (Kleiber, 1975; postabsorptive, resting motionless and at thermoneutrality) with the exception that the animals were still juveniles. Therefore, the mean $\dot{V}o_2$ was considered an estimate of RMR for juvenile animals and then used as a base level to compare with postprandial metabolic rate.

2.2. Postprandial metabolic rate and estimation of HIF

To determine the increase in metabolic rate associated with digestion, assimilation and nutrient interconversion, experimental runs were also performed under postprandial conditions. Postprandial measurements commenced 30 min after a meal of approximately 75% of the normal daily food intake (kg day^{-1}) of white croaker (*Micropogonias furnieri*), striped weakfish (*Cynoscion guatucupa*) and Brazilian menhaden (*Brevoortia aurea*). Similar to postabsortive conditions, data were obtained under thermoneutrality, and $\dot{V}o_2$ measurements consisted of at least 10 min (range = 10–51) of continuous resting behavior (lying motionless) and a steady rate of oxygen consumption. The total number of $\dot{V}o_2$ measurements per session varied among animals according to their particular behavior.

Due to the limited period in which wild animals could be kept in the metabolic box, experimental runs could not be performed longer than 3 h, which resulted in a total time of 3.5 h after feeding for postprandial measurements. As a result, the full duration of an elevated postprandial metabolic rate could not be recorded, and HIF could not be estimated as the total oxygen consumed during the complete process. As an alternative approach, we estimated the mean postprandial increase (expressed as a percentage) in metabolism above postabsorptive levels for the initial 3.5 h after meal ingestion. A similar definition of HIF was previously used with Steller sea lions by Rosen and Trites (1997, 2003), who found that metabolism peaks 2.8–3.7 h after feeding depending on meal size and returns to fasting levels between 6 and 10 h. Therefore, our HIF estimation probably represents the first half of the complete process (*see Discussion*). To examine variations in $\dot{V}o_2$ within the initial 3.5 h postprandial, the elapsed time since the animal was fed (30 min after experimental run started) and the beginning of each of the postprandial $\dot{V}o_2$ measurements was recorded as the variable *time from feeding* (in min) and included in the statistical analysis.

2.3. Statistical analysis

Prior to analysis, graphical explanatory techniques were applied to the original data to identify outliers both in the response variable ($\dot{V}o_2$) and continuous explanatory variables. The assessment of collinearity–correlation between explanatory variables used in both statistical models applied (*feeding condition*, *animal ID*, *body mass*, *month*, *experimental run* and *time from feeding*) was performed using multiple pair-wise scatter plots (pair plots) (Zuur et al., 2010). Variables such as *age and sex* were not considered because all animals were juvenile males.

Linear mixed effect models (LME; Pinheiro and Bates, 2000; West et al., 2006; Zuur et al., 2007, 2009) were used to estimate the mass specific oxygen consumption rate ($\dot{V}o_2$) in relation to both *feeding conditions* (postabsorptive and postprandial). Data were two-way nested (*experimental run* is nested in *animal ID*), which means that observations