



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



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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  $17.93 \pm 1.84$  and  $11.15 \pm 1.91$  mL O<sub>2</sub> min<sup>-1</sup> kg<sup>-1</sup>, 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.

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### 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.

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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  $13.2 \pm 1.3$  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<sup>-1</sup>. 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<sub>2</sub> min<sup>-1</sup> kg<sup>-1</sup>) 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<sub>2</sub> produced per unit of O<sub>2</sub> consumed) performed in Antarctic fur seals *Arctocephalus gazella* (Arnould et al., 2001). During calibration, oxygen concentrations in the metabolic box were  $99.29 \pm 0.04\%$  and  $99.52 \pm 0.02\%$  of the predicted values for N<sub>2</sub> flows of 2 l min<sup>-1</sup> and 5 l min<sup>-1</sup>, 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 ( $18.3 \pm 2.4$  °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<sup>-1</sup>) of white croaker (*Micropogonias furnieri*), striped weakfish (*Cynoscion guatucupa*) and Brazilian menhaden (*Brevoortia aurea*). Similar to postabsorptive 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

within the same experimental run were likely to be correlated, but correlation between  $\dot{V}O_2$  measurements for the same animal was also expected. This resulted in the following model:

$$\dot{V}O_{2ijk} = \alpha + \text{feeding condition}_{ijk} + a_k + a_{j/k} + \varepsilon_{ijk}$$

where  $\dot{V}O_{2ijk}$  is the mass specific oxygen consumption for observation  $i$  in experimental run  $j$  of animal  $k$ , where  $i$  refers to the observation within an experimental run that takes any value between 2 and 7,  $j$  refers to experimental runs ( $j = 3, \dots, 5$ ) and  $k$  to animal ( $k = 1, \dots, 5$ ). The explanatory variable *feeding condition* is nominal and has two classes (postabsorptive and postprandial). The term  $a_{j/k}$  is the random effect *experimental run* that is nested within the random effect *animal ID* ( $a_k$ ). Both are assumed to be normally distributed with mean 0 and variance  $\sigma^2$ . The expression  $\varepsilon_{ijk}$  is the unexplained error and represents the variation within experimental runs. It was assumed to be normally distributed mean 0 and variance  $\sigma^2$ . The variables *month* and *body mass* were excluded from this model due to collinearity with *experimental run*.

A similar model was applied to the postprandial data to test for the effect of *time from feeding* on  $\dot{V}O_2$ . In this case, we applied LME on one-way nested data modeling *animal ID* as a random effect and factor *month* as fixed. Although two experimental runs per animal are a small number of clusters for the use of a random intercept, it is also too many for the fixed part. The two experimental runs per animal were taken in March and April, respectively. Hence, we decided to use factor *month* as fixed to reduce the number of parameters due to small sample size (Zuur et al., 2013). This resulted in the following model:

$$\dot{V}O_{2ij} = \alpha + \text{time from feeding}_{ij} + f_{\text{month}}h_{ij} + a_j + \varepsilon_{ij}$$

where  $\dot{V}O_{2ij}$  is the mass specific oxygen consumption of observation  $i$  of animal  $j$ , where  $j$  runs from 1 to 5, and  $i$  takes any value between 8 and 12. The notation above means that  $\dot{V}O_{2ij}$  is modeled as a function of time (*time from feeding*) and factor *month* (March and April). The term  $a_j$  was the random intercept animal and was assumed to be normally distributed with mean 0 and variance  $\sigma^2_{\text{animal}}$ . The residual  $\varepsilon_{ij}$  was also assumed to be normally distributed with mean 0 and variance  $\sigma^2$ .

The model selection followed the step-down approach described by West et al., 2006; Zuur et al., 2009. All analyses were performed with R (R Development Core Team, 2012) using the nlme Package (Pinheiro et al., 2012). Optimal models were validated to confirm that the

underlying statistical assumptions were not violated; normality of residuals was assessed by plotting theoretical quantiles versus standardized residuals (Q-Q plots), and homogeneity of variance was evaluated by plotting residual versus fitted values. Independence was examined by plotting residuals versus time (Zuur et al., 2009).

### 3. Results

A total of 76 measurements (29 postabsorptive and 47 postprandial) of in air resting metabolic rate were conducted (Table 1). Although they were performed under both feeding conditions in the five SAFS, data from one postabsorptive animal could not be used due to file corruption. Durations of  $\dot{V}O_2$  measurements ranged from 10 to 24 min ( $14.3 \pm 4.1$  s.d.) and from 10 to 51 min ( $23.2 \pm 10.2$  s.d.) for the postabsorptive and postprandial conditions, respectively.

The estimated mean values of RMR for the postabsorptive and postprandial conditions obtained by the random intercept model were  $11.15 \pm 1.91$  and  $17.93 \pm 1.84$  mL O<sub>2</sub> min<sup>-1</sup> kg<sup>-1</sup>, respectively. The amount of variation around the intercept ( $\sigma^2_{\text{animal}}$ ) was  $(3.65)^2$ . The variance ( $\sigma^2_{\text{Exp-run}}$ ), which allowed for a random variation among experimental runs for each animal, was  $(2.50)^2$ , indicating that both random effects were needed in the model. Using a likelihood ratio test, models with and without the factor *feeding condition* were compared, and the results showed that the variable *feeding condition* was highly significant ( $L = 16.67$ ,  $df = 1$ ,  $p < 0.001$ ). The mean postprandial increase in metabolism above postabsorptive levels was 61%, which we attribute to the HIF during the first 3.5 h after feeding.

When only postprandial data were analyzed, modeling results confirmed that neither *time from feeding* nor *month* were significantly related to the response variable ( $\dot{V}O_2$ ), indicating that the overall increase in metabolic rate over postabsorptive levels did not vary significantly during the first 3.5 h after feeding and between the two time periods.

### 4. Discussion

This study provides the first estimate of in air RMR and HIF in the SAFS and was measured in wild animals temporally habituated to captivity. Although the estimated HIF does not represent the complete digestion period, the results showed a significant (61%) increase in resting metabolism that should be considered in any energy budget for juvenile SAFS foraging at-sea.

**Table 1**  
Measurements of resting metabolic rate (RMR) from five wild juvenile South American fur seal males in postabsorptive (PA) and postprandial (PP) feeding conditions.

Animal ID	Feeding condition	Experimental run (date)	RMR in mL O <sub>2</sub> min <sup>-1</sup> kg <sup>-1</sup> (time since beginning of the experimental run*, in min)						
			1#	2#	3#	4#	5#	6#	7#
FMM1	PA	1 (26-Mar)	18.3 (6)	19.5 (36)	16.5 (54)	18.6 (85)	18.6 (116)		
		2 (28-Mar)	12.3 (30)	14.7 (41)	14.0 (59)	13.1 (72)	13.6 (96)		
	PP	3 (24-Mar)	22.4 (48)	26.0 (90)	25.0 (141)				
		4 (05-Apr)	20.5 (43)	22.2 (80)	24.7 (118)	26.5 (162)	23.7 (198)	20.7 (240)	
FMM2	PA	1 (29-Mar)	6.9 (47)	6.5 (67)	9.7 (84)				
		2 (06-Apr)	10.0 (52)	9.2 (60)					
		3 (07-Apr)	10.3 (18)	9.2 (36)					
	PP	4 (30-Mar)	23.9 (41)	20.0 (66)	17.9 (90)	19.3 (114)			
		5 (08-Apr)	13.1 (41)	9.2 (60)	12.7 (78)	14.0 (93)	10.7 (114)		
FMM3	PA	1 (21-Mar)	6.2 (26)	4.7 (46)	4.5 (99)	4.8 (121)			
		2 (09-Apr)	10.4 (29)	10.6 (55)					
	PP	3 (23-Mar)	9.7 (31)	10.5 (44)	13.3 (50)	12.7 (74)	12.3 (104)	8.4 (136)	7.8 (166)
		4 (01-Apr)	12.0 (62)	11.2 (92)	11.5 (127)	13.0 (162)	14.6 (191)		
FMM4	PA	1 (22-Mar)	11.9 (6)	8.5 (24)	11.2 (36)	6.9 (48)			
		2 (03-Apr)	15.4 (6)	11.8 (36)					
	PP	3 (25-Mar)	21.1 (42)	15.8 (60)	17.7 (84)	17.4 (108)	16.4 (132)		
FMM5	PP	4 (02-Apr)	20.6 (38)	23.5 (54)	20.8 (65)				
		1 (27-Mar)	17.7 (46)	17.4 (60)	20.0 (78)	20.9 (90)			
		2 (04-Apr)	18.5 (39)	17.3 (54)	19.9 (72)	20.5 (90)	16.9 (108)		

\* To represent the *Time from feeding*, 30 min has been added to the *time since beginning of the experimental run* in PP measurements.

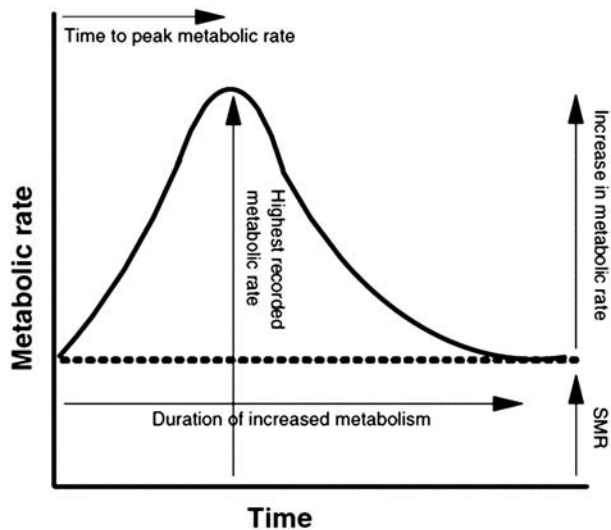


Fig. 1. Schematic illustration of several metrics used to quantify the HIF (*Heat increment of feeding*) or the SDA (*Specific Dynamic Action*) response (extracted from McCue, 2006).

The postabsorptive RMR ( $11.1 \text{ mL O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ) was 2.1 times higher than the BMR predicted for terrestrial mammals of similar body mass (Kleiber, 1975). This result is consistent with estimates from other pinnipeds and sea otters (*Enhydra lutris*) in which RMR is 2–3 times greater than predicted (Matsuura and Whittow, 1973; Miller, 1974; Costa, 1982; Davis et al., 1985; Costa and Gentry, 1986; Feldkamp, 1987; Davis et al., 1988; Williams et al., 1988; Costa et al., 1989a; 1989b; Liao, 1990; Ponganis et al., 1991; Boyd et al., 1995; Hurley and Costa, 2001; Costa and Gales, 2003; Dassis et al., 2012a). The reason for an elevated RMR relative to terrestrial mammals is not understood, but it may be associated with adaptations for thermoregulation in water, which has a thermal conductance at least 25-fold greater than air (Schmidt-Nielsen, 1979). Although marine mammals have a RMR that is higher than that in terrestrial mammals, the younger animals used in this study may have resulted in an additional increase (Davydov and Marakova, 1965; Matsuura and Whittow, 1973; Miller and Irving, 1975; Øritsland and Ronald, 1975; Ashwell-Erickson and Elsner, 1981; Thompson et al., 1987; Rea and Costa, 1992). Causes for an elevated resting metabolic rate in young animals may be related to growth, smaller body size and the concomitant maturation of thermoregulatory ability (Brody, 1945; Donohue et al., 2000).

Our results indicate that juvenile SAFS experience high maintenance energetic costs that may affect their field metabolic rate (FMR) while at sea, foraging ecology and survival rates. In addition to this elevated

RMR, HIF increases the metabolism an additional 61%. Since the HIF is an increase in energy expenditure following feeding, it can be characterized using metrics related to the typical postprandial metabolic curve (McCue, 2006; Fig. 1). Although we were not able to measure the complete HIF postprandial period, our results allowed us to estimate minimum values of these metrics for juvenile SAFS.

Considering that the postprandial increase in metabolic rate was apparent within the first 30 min after feeding and remained stable for at least the next three hours (no significant effect of *Time from feeding*), we estimated: 1) the *Time to peak metabolic rate* to be at least 30 min, 2) the *Highest recorded metabolic rate* as  $17.9 \text{ mL O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ , 3) the *Increase in metabolic rate* as  $6.8 \text{ mL O}_2 \text{ min}^{-1} \text{ kg}^{-1}$  (the difference between postabsorptive and postprandial fitted  $\dot{V}\text{O}_2$ ) and 4) the total *Duration of increased metabolism* as a minimum of 3.5 h. Considering that total HIF duration in mammals is between 2 and 8 h (Rosen and Trites, 1997; McCue, 2006), we hypothesize that the 3.5 h of maintained increased metabolism represents the first half of the complete HIF period for juvenile SAFS (which might extend to a total time of approximately 6–7 h).

Comparison with previous studies is difficult because of the different ways in which HIF is expressed. However, we can compare our estimate when postprandial energy consumption is expressed as a multiple of RMR, a metric that is known as the SDA scope (Specific dynamic action scope; see McCue, 2006). SDA scope is calculated as the maximal postprandial metabolic rate divided by the standard or basal metabolic rate. The SDA scope is important because it can be compared to the maximal metabolic scope of an animal to estimate the residual capacity for activity during digestion (McCue, 2006). The estimated SDA scope for juvenile SAFS was 1.6, which was the same as the SDA scope measured in northern fur seal pups resting within their thermal neutral zone (Livanag, 2010) and included within the range of values measured for other pinnipeds and sea otters (Table 2). The similarity among SDA scopes reported for different marine mammal species supports our HIF estimate measured during the first 3.5 h after feeding probably represents the maximum increase in metabolic rate.

Some studies have suggested that HIF may augment thermogenic heat production in cold-stressed endotherms (Bech and Praesteng, 2004). This augmentation would reduce the need for thermoregulatory heat production at low ambient temperatures. Current results regarding this hypothesis differ by species. While heat substitution by HIF has been documented in some species of mammals (Simek, 1975; Masman et al., 1988; MacArthur and Campbell, 1994; Chappell et al., 1997; Jensen et al., 1999), other studies have not found convincing evidences for the substitution (Klaassen et al., 1989; Campbell et al., 2000; Hindle et al., 2003). With regard to marine mammals, no evidence of heat substitution from HIF was found in Steller sea lions (Rosen and Trites, 2003), but data obtained from sea otters (Costa and Kooyman,

Table 2  
SDA (*Specific Dynamic Action*) scope of different species of pinnipeds and sea otters.

	Species	SDA scope	Data source
Otariids	South American fur seal	1.6	This study
	<i>Arctocephalus australis</i>		
	Northern fur seal	1.6	Livanag (2010)
	<i>Callorhinus ursinus</i>		
	Steller sea lions	1.7 to 2.1	Rosen and Trites (1997)
Phocids	<i>Eumetopias jubatus</i>		
	Northern elephant seals	1.4 to 1.6	Barbour (1993)
	<i>Mirounga angustirostris</i>		
	Harp seal	1.4 to 1.7	Gallivan and Ronald (1981)
	<i>Phoca groenlandica</i>		
	Ring seal	1.8 to 2	Parsons (1977)
	<i>Phoca hispida</i>		
	Harbor seal	1.3 to 1.9	Ashwell-Erickson and Elsner (1981), Markussen et al. (1994)
Sea otters	<i>Phoca vitulina</i>		
	Sea otter	1.5	Costa and Kooyman (1984)
	<i>Enhydra lutris</i>		

1984) have supported augmentation, which was suggested to be correlated with the long period of resting at-sea observed in this species.

Our study was performed over a small range of air temperatures that were within the likely thermoneutral zone of SAFS, so it does not provide evidence for the thermoregulatory role of HIF. In addition, differences between fasting and postprandial metabolic rates cannot be directly extrapolated from *in air* to *in water* measurements. However, the typical at-sea behavior of these animals, characterized by long periods of resting at the surface during foraging trips (Gentry and Kooyman, 1986; Liwanag, 2010; Dassis et al., 2012b), might support the substitution hypothesis. SAFS usually spend prolonged periods resting at-sea (Gentry and Kooyman, 1986; Liwanag, 2010; Dassis et al., 2012b), a behavior that has been interpreted as a thermoregulation challenge (Liwanag et al., 2009; Liwanag, 2010). In this scenario, the increased production of heat associated with digestion when resting in air—that might be occurring in a similarly range of values when resting in water—could be used to maintain body temperature during long periods of resting on the sea surface. The thermoregulatory advantages implied in the substitution hypothesis may be more important in juveniles, which have a higher surface to volume ratio and in which energetic efficiency is further constrained by inexperience and the incomplete development of foraging skills.

This study has provided the first estimation of in air RMR and HIF in SAFS and showed the need of further research to determinate the total duration of HIF and its role in thermoregulation and FMR at sea. These estimations are important variables in bio-energetic models used to estimate FMR in different geographical regions and seasons.

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## References

- Arnould, J.P.Y., Green, J.A., Rawlins, D.R., 2001. Fasting metabolism in Antarctic fur seal (*Arctocephalus gazella*) pups. *Comp. Biochem. Physiol. A* 129, 829–841.
- Ashwell-Erickson, S., Elsner, R., 1981. The energy cost of Free-Existence for Bering Sea Harbor and Spotted Seals. In: Hood, D.W., Calder, J.A. (Eds.), *Eastern Bering Sea Shelf: Oceanography and Resources*, vol. 2. University of Washington Press, Seattle, pp. 869–899.
- Barbour, A.S., 1993. Heat Increment of Feeding in Juvenile Northern Elephant Seals. (MSc. thesis) University of California, Santa Cruz, Santa Cruz, CA (47 pp.).
- Bastida, R., Rodríguez, D., 2003. *Mamíferos Marinos de Patagonia y Antártida*. Vázquez Mazzini Editores, Buenos Aires.
- Bech, C., Praesteng, C.E., 2004. Thermoregulatory use of heat increment of feeding in the tawny owl (*Strix aluco*). *J. Therm. Biol.* 29, 649–654.
- Bowen, W.D., 1997. Role of marine mammals in aquatic ecosystems. *Mar. Ecol. Prog. Ser.* 158, 267–274.
- Boyd, L.L., Woakes, A.J., Butler, P.J., Davis, R.W., Williams, T.M., 1995. Validation of heart rate and doubly labeled water as measures of metabolic rate during swimming in California sea lions. *Funct. Ecol.* 9, 151–160.
- Brody, S., 1945. *Bioenergetics and Growth*. Hafner Press, London.
- Busk, M., Overgaard, J., Hicks, J.W., Bennett, A.F., Wang, T., 2000. Effects of feeding on arterial blood gases in the American alligator *Alligator mississippiensis*. *J. Exp. Biol.* 203, 3117–3124.
- Campbell, K.L., McIntyre, I.W., MacArthur, R.A., 2000. Postprandial heat increment does not substitute for active thermogenesis in cold-challenged star-nosed moles (*Condylura cristata*). *J. Exp. Biol.* 203, 301–310.
- Chakraborty, S.C., Ross, L.G., Ross, B., 1992. Specific dynamic action and feeding metabolism in common carp *Cyprinus carpio* L. *Comp. Biochem. Physiol. A* 103, 809–815.
- Chappell, M.A., Bachman, G.C., Hammond, K.A., 1997. The heat increment of feeding in house wren chicks: magnitude, duration, and substitution for thermostatic costs. *J. Comp. Physiol.* 167B, 313–318.
- Costa, D.P., 1982. Energy, nitrogen and electrolyte flux and sea-water drinking in the sea otter (*Enhydra lutris*). *Physiol. Zool.* 55, 35–44.
- Costa, D.P., 2008. A model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals. *Aquat. Conserv.* 17, S44–S52.
- Costa, D.P., Gales, N.J., 2003. Energetics of a benthic diver: seasonal foraging ecology of the Australian sea lion, *Neophoca cinerea*. *Ecol. Monogr.* 73 (1), 27–43.
- Costa, D.P., Gentry, R.L., 1986. Free-Ranging Energetic of Northern Fur Seals. In: Gentry, R.L., Kooyman, G.L. (Eds.), *Fur Seals: Maternal Strategies on Land and at Sea*. Princeton University Press, Princeton, pp. 79–101.
- Costa, D.P., Kooyman, G.L., 1984. Contribution of specific dynamic action to heat balance and thermoregulation in the sea otter *Enhydra lutris*. *Physiol. Zool.* 57, 199–203.
- Costa, D.P., Croxall, J.P., Duck, C.D., 1989a. Foraging energetic of Antarctic fur seals in relation to prey availability. *Ecology* 70, 596–606.
- Costa, D.P., Kretzmann, M., Thorson, P.H., 1989b. Diving pattern and energetic of the Australian sea lion, *Neophoca cinerea*. *Am. Zool.* 29 (4), 71A.
- Dassis, M.D., Rodríguez, D.H., Ieno, E.N., Davis, R.W., 2012a. Submerged swimming and resting metabolic rates in Southern sea lions. *J. Exp. Mar. Biol. Ecol.* 432–433, 106–112.
- Dassis, M.D., Farenga, M.O., Bastida, R.O., Rodríguez, D.H., 2012b. At-sea behavior of South American fur seals: influence of coastal hydrographic conditions and physiological implication. *Mamm. Biol.* 77, 47–52.
- Davis, R.W., Williams, T.M., Kooyman, G.L., 1985. Swimming metabolism of yearling and adult harbor seals *Phoca vitulina*. *Physiol. Zool.* 58 (5), 590–596.
- Davis, R.W., Williams, T.M., Thomas, J.A., Kastelein, R.A., Cornell, L.H., 1988. The effects of oil contamination and cleaning on sea otters (*Enhydra lutris*). II. Metabolism, thermoregulation, and behavior. *Can. J. Zool.* 66, 2782–2790.
- Davydov, A., Marakova, A., 1965. Changes in heat regulation and circulation in newborn seals on transition to aquatic form of life. *Fed. Proc.* 24, 563–566.
- Depocas, F., Hart, J.S., 1957. Use of the Pauling oxygen analyzer for measurements of oxygen consumption of animals in open-circuit systems and in short-lag, close circuit apparatus. *J. Appl. Physiol.* 10, 388–392.
- Development Core Team, R., 2012. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria3-900051-07-0 (URL <http://www.R-project.org/>).
- Doight, C.E., Croxall, J.P., 1985. Diet and Energy Budget of the Antarctic Fur Seal, *Arctocephalus gazella*, at South Georgia. In: Siegfried, W.R., Condy, P.R., Laws, R.M. (Eds.), *Antarctic nutrient cycles and food webs*. Springer-Verlag, Berlin, pp. 543–550.
- Donohue, M.J., Costa, D.P., Goebel, M.E., Baker, J.D., 2000. The ontogeny of metabolic rate and thermoregulatory capabilities of northern fur seal, *Callorhinus ursinus*, pups in air and water. *J. Exp. Biol.* 203, 1003–1016.
- Enders, E.C., Scruton, D.A., 2006. Potential application of bioenergetics models to habitat modeling and importance of appropriate metabolic rate estimates with special consideration for Atlantic salmon. *Can. Tech. Rep. Fish. Aquat. Sci.* 2641, 40.
- Enstipp, M.R., Grémillet, D., Jones, D.R., 2008. Heat increment of feeding in double-crested cormorants (*Phalacrocorax auritus*) and its potential for thermal substitution. *J. Exp. Biol.* 211, 49–57.
- Feldkamp, S.D., 1987. Swimming in the California sea lion: morphometrics, drag and energetic. *J. Exp. Biol.* 131, 117–135.
- Gallivan, G.J., Ronald, K., 1981. Apparent specific dynamic action in the harp seal (*Phoca groenlandica*). *Comp. Biochem. Physiol.* 69A, 579–581.
- Gentry, R.L., Kooyman, G.L., 1986. Introduction. In: Gentry, R.L., Kooyman, G.L. (Eds.), *Fur seals: maternal strategies on land and at sea*. Princeton University Press, Princeton, pp. 3–27.
- Hamada, A., Maeda, W., 1983. Oxygen uptake due to specific dynamic action in the carp, *Cyprinus carpio*. *Jpn. J. Limnol.* 44, 225–239.
- Härkönen, T., Heide-Jørgensen, M.P., 1991. The harbour seal *Phoca vitulina* as a predator in the Skagerrak. *Ophelia* 34, 191–207.
- Hiby, A.R., Harwood, J., 1985. The Effects of Variation in Population Parameters on the Energy Requirements of a Hypothetical Grey Seal Population. In: Beddington, J.R., Beverton, J.H., Lavigne, D.M. (Eds.), *Marine mammals and fisheries*. George Allen & Unwin, London, pp. 337–343.
- Hicks, J.W., Wang, T., Bennett, A.F., 2000. Patterns of cardiovascular and ventilatory response to elevated metabolic states in the lizard *Varanus exanthematicus*. *J. Exp. Zool.* 203, 2437–2445.
- Hindle, A.G., McIntyre, I.W., Campbell, K.L., MacArthur, R.A., 2003. The heat increment of feeding and its thermoregulatory implication in the short-tailed shrew (*Blarina brevicauda*). *Can. J. Zool.* 81, 1445–1453.
- Hinga, K.R., 1979. The food requirements of whales in the southern hemisphere. *Deep-Sea Res.* A 26, 569–577.
- Hopkins, W.A., Roe, J.H., Phillip, T., Congdon, J.D., 1999. Digestive metabolism in banded water snakes, *Nerodia fasciata*. *Am. Zool.* 39, 95A–96A.
- Hurley, J.A., Costa, D.P., 2001. Standard metabolic rate at the surface and during trained submersions in adult California sea lions (*Zalophus californianus*). *J. Exp. Biol.* 204, 3273–3281.
- Janes, D.N., Chappell, M.A., 1995. The effect of ration size and body size on specific dynamic action in adelic penguin chicks, *Pygoscelis adeliae*. *Physiol. Zool.* 68, 1029–1044.
- Jensen, P.G., Pekins, P.J., Holter, J.B., 1999. Compensatory effect of the heat increment of feeding on thermoregulation costs of white-tailed deer fawns in winter. *Can. J. Zool.* 77, 1474–1485.
- Klaassen, M., Bech, C., Slagsvold, G., 1989. Basal metabolic rate and thermal conductance in growing Arctic tern chicks (*Sterna paradisaea*) and the effect of heat increment of feeding on thermoregulatory expenses. *Ardea* 77, 193–200.
- Kleiber, M., 1975. *The Fire of Life, and Introduction to Animal Energetics*. Robert E. Krieger Publishing Company, New York.
- Kriss, M., 1938. The specific dynamic effects of proteins when added in different amounts to a maintenance diet. *J. Nutr.* 15, 565–581.

- Kriss, M., Marcy, L.F., 1940. The metabolism of tyrosine, aspartic acid and asparagine, with special reference to respiratory exchange and heat production. *J. Nutr.* 19, 297–309.
- Kriss, M., Forbes, E.B., Miller, R.C., 1934. The specific dynamic effects of protein, fat, and carbohydrate as determined with the albino rat at different planes of nutrition. *J. Nutr.* 8, 509–534.
- Lavigne, D.M., Innes, S., Stewart, R.E.A., Worthy, G.A.J., 1985. An Annual Energy Budget for north-west Atlantic Harp Seals. In: Beddington, R.J.H., Beverton, R.J.H., Lavigne, D.M. (Eds.), *Marine mammals and fisheries*. George Allen & Unwin, London, pp. 319–336.
- Lavigne, D.M., Innes, S., Worthy, G.A.J., Kovacs, K.M., Schmitz, O.J., Hickie, J.P., 1986. Metabolic rates of seals and whales. *Can. J. Zool.* 64 (2), 279–284.
- Liao, J.A., 1990. An Investigation of the Effect of Water Temperature on the Metabolic Rate of the California Sea Lion (*Zalophus californianus*). (MSc diss) University of California, Santa Cruz.
- Liwanag, H.E.M., 2010. Energetic costs and thermoregulation in Northern Fur Seal (*Callorhinus ursinus*) Pups: the importance of behavioral strategies for thermal balance in furred marine mammals. *Physiol. Biochem. Zool.* 83 (6), 898–910.
- Liwanag, H.E.M., Williams, T.M., Costa, D.P., Kanatous, S.B., Davis, R.W., Boyd, I.L., 2009. The effects of water temperature on the energetic costs of juvenile and adult California sea lions (*Zalophus californianus*): the importance of skeletal muscle thermogenesis for thermal balance. *J. Exp. Biol.* 212, 3977–3984.
- Lusk, G., 1910. An attempt to discover the cause of the specific dynamic action of protein. *Proc. Soc. Exp. Biol. Med.* 7, 136–137.
- Lusk, G., 1912–1913ab. The influence of the ingestion of amino-acids upon metabolism. *J. Biol. Chem.* 13, 155–183.
- Lusk, G., 1912–1913bc. Metabolism after the ingestion of dextrose and fat, including the behavior of water, urea and sodium chloride solutions. *J. Biol. Chem.* 13, 27–47.
- Lusk, G., 1915. An investigation into the causes of the specific dynamic action of the food-stuffs. *J. Biol. Chem.* 20, 555–617.
- Lusk, G., 1922. The specific dynamic action of various food factors. *Medicine* 1, 311–354.
- MacArthur, R.A., Campbell, K.L., 1994. Heat increment of feeding and its thermoregulatory benefit in the muskrat (*Ondatra zibethicus*). *J. Comp. Physiol. B* 164, 141–146.
- Markussen, N.H., Øritsland, N.A., 1991. Food energy requirements of the harp seal (*Phoca groenlandica*) population in the Barents and White Seas. *Polar Res.* 10, 603–608.
- Markussen, N.H., Ryg, M., Lydersen, C., 1992. Food consumption of the NE Atlantic minke whale (*Balaenoptera acutorostrata*) population estimated with a simulation model. *ICES J. Mar. Sci.* 49, 317–323.
- Markussen, N.H., Ryg, M., Øritsland, N.A., 1994. The effect of feeding on the metabolic rate in harbour seals (*Phoca vitulina*). *J. Comp. Physiol.* 164B, 89–93.
- Masman, D., Daan, S., Dietz, M., 1988. Heat Increment of Feeding in the Kestrel, *Falco tinnunculus*, and its Natural Seasonal Variation. In: Bech, C., Reinertsen, R.E. (Eds.), *Physiology of Cold Adaptation in Birds*. Plenum, New York, pp. 123–135.
- Matsuura, D.T., Whittow, G.C., 1973. Oxygen uptake of the California sea lion and harbor seal during exposure to heat. *Am. J. Physiol.* 225, 711–715.
- Maynard, A.L., Loosli, K.J., 1969. *Animal Nutrition*, 5th edn. McGraw Hill, New York.
- McCue, M.D., 2006. Specific dynamic action: a century of investigation. *Comp. Biochem. Physiol. A* 144, 381–394.
- Miller, D.J., 1974. The Sea Otter *Enhydra lutris*: Its Life History, Taxonomic Status and Some Ecological Relationships. California Department of Fish and Game Marine Resources Leaflet No. 7.
- Miller, K., Irving, L., 1975. Metabolism and temperature regulation in young harbor seals *Phoca vitulina richardi*. *Am. J. Physiol.* 229, 506–511.
- Mohn, R., Bowen, W.D., 1996. Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. *Can. J. Fish. Aquat. Sci.* 53, 2722–2738.
- Muir, B.S., Niimi, A.J., 1972. Oxygen consumption of the euryhaline fish wholehole (*Kuhlia sandvicensis*) with reference to salinity, swimming, and food consumption. *J. Fish. Res. Board Can.* 29, 67–77.
- Naumov, A.G., Chekunova, V.I., 1980. Energy requirements of pinnipeds (Pinnepedia). *Oceanology* 20, 348–350.
- Nespolo, R.F., Bacigalupe, L.D., Bozinovic, F., 2003. The influence of heat increment of feeding on basal metabolic rate in *Phyllotis darwini* (Muridae). *Comp. Biochem. Physiol. A* 134, 139–145.
- Olesiuk, P.F., 1993. Annual prey consumption by harbor seals (*Phoca vitulina*) in the Strait of Georgia, British Columbia. *Fish. Bull.* 91, 491–515.
- Øritsland, N.A., Markussen, N.H., 1990. Outline of a physiologically based model for population energetics. *Ecol. Model.* 52, 267–288.
- Øritsland, N.A., Ronald, K., 1975. Effect of solar radiation and wind chill on skin temperature of the harp seal, *Pagophilus groenlandicus* (Erxleben, 1777). *Comp. Biochem. Physiol. A* 44, 519–525.
- Overgaard, J., Busk, M., Hicks, J.W., Jensen, F.B., 1999. Respiratory consequences of feeding in the snake Python molurus. *Comp. Biochem. Physiol. A* 124, 359–365.
- Parsons, J.L., 1977. *Metabolic Studies on Ringed Seals (Phoca hispida)*. (MS. Thesis) University of Guelph, Guelph, Ontario, Canada 82.
- Pinheiro, J., Bates, D., 2000. *Mixed Effects Models in S and S-Plus*. Springer-Verlag, New York.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core team, 2012. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1–103.
- Ponce de León, A., Pin, O.D., 2006. Distribución, Reproducción y Alimentación del Lobo Fino *Arctocephalus australis* y del León Marino *Otaria flavescens* en Uruguay. In: Menafrá, R., Rodríguez-Gallego, L., Scarabino, F., Conde, D. (Eds.), *Bases para la conservación y el manejo de la costa uruguaya*. Vida Silvestre, Uruguay, Montevideo, pp. 305–314.
- Pongonis, P.J., Kooyman, G.L., Zornow, M.H., 1991. Cardiac output in swimming California sea lions, *Zalophus californianus*. *Physiol. Zool.* 64 (5), 1296–1306.
- Rea, L.D., Costa, D., 1992. Changes in standard metabolism during long-term fasting in northern elephant seal pups (*Miroounga angustirostris*). *Physiol. Zool.* 65, 97–111.
- Roe, J.H., Hopkins, W.A., Snodgrass, J.W., Congdon, J.D., 2004. The influence of circadian rhythms on pre- and post-prandial metabolism in the snake *Lamprophis fuliginosus*. *Comp. Biochem. Physiol. A* 139, 159–168.
- Rosen, D.A.S., Trites, A.W., 1997. Heat increment of feeding in Steller sea lions, *Eumetopias jubatus*. *Comp. Biochem. Physiol. A* 118 (3), 877–881.
- Rosen, D.A.S., Trites, A.W., 2003. No evidence for bioenergetic interaction between digestion and thermoregulation in Steller sea lions *Eumetopias jubatus*. *Physiol. Biochem. Zool.* 76 (6), 899–906.
- Rubner, M., 1902. *Die Gesetze des Energieverbrauchs bei der Ernährung*. Dauticke, Leipzig.
- Ryg, M., Øritsland, N.A., 1991. Estimates of energy expenditure and energy consumption of ringed seals (*Phoca hispida*) throughout the year. *Polar Res.* 10, 595–601.
- Schmidt-Nielsen, K., 1979. *Animal Physiology: Adaptation and Environment*, 2nd ed. Cambridge University Press, New York.
- Secor, S.M., 2003. Gastric function and its contribution to the postprandial metabolic response of the Burmese python *Python molurus*. *J. Exp. Biol.* 206, 1621–1630.
- Secor, S.M., Phillips, J.A., 1997. Specific dynamic action of a large carnivorous lizard *Varanus albigularis*. *Comp. Biochem. Physiol. A* 117, 515–522.
- Simek, V., 1975. Specific dynamic action of a high-protein diet and its significance for thermoregulation in the golden hamster. *Physiol. Bohemoslov.* 24, 421–424.
- Stenson, G.B., Hammill, M.O., Lawson, J.W., 1997. Predation by harp seals in Atlantic Canada: preliminary consumption estimates for Arctic cod, capelin and Atlantic cod. *J. Northwest Atl. Fish. Sci.* 22, 137–154.
- Thompson, S.D., Ono, K.A., Oftedal, O.T., Boness, D.J., 1987. Thermoregulation and resting metabolic rate of California sea lion (*Zalophus californianus*) pups. *Physiol. Zool.* 60, 730–736.
- Ugland, K.I., Jødestøl, K.A., Aspholm, P.E., Krøyer, A.B., Jakobsen, T., 1993. Fish consumption by invading harp seals off the Norwegian coast in 1987 and 1988. *ICES J. Mar. Sci.* 50, 27–38.
- Vaz-Ferreira, R., 1982. *Arctocephalus australis* (Zimmermann), South American fur seal. *FAO Fish. Ser.* 4, 497–508.
- Vaz-Ferreira, R., Ponce de León, A., 1987. South American Fur Seal, *Arctocephalus australis*, in Uruguay. In: Croxall, J.P., Gentry, R.L. (Eds.), *Status, biology and ecology of fur seals*. NOAA Tech. Rep. 51, pp. 29–32.
- West, B.T., Welch, B., Galecki, A.T., 2006. *Linear Mixed Models: A Practical Guide Using Statistical Software*. Chapman and Hall/CRC.
- Wilhelmj, C.M., Bollman, J.L., 1928. The specific dynamic action and nitrogen elimination following intravenous administration of various amino acids. *J. Biol. Chem.* 77, 127–149.
- Wilhelmj, C.M., Bollman, J.L., Mann, F.C., 1931. A study of certain factors concerned in the specific dynamic action of amino acids administered intravenously and a comparison with oral administration. *Am. J. Physiol.* 98, 1–17.
- Williams, T.M., Kastelein, R.A., Davis, R.W., Thomas, J.A., 1988. The effects of oil contamination and cleaning in sea otters (*Enhydra lutris*). I. Thermoregulatory implications based on pelt studies. *Can. J. Zool.* 66, 2776–2781.
- Winship, A.J., Trites, A.W., Rosen, D.A.S., 2002. A bioenergetic model for estimating the food requirements of Steller sea lions *Eumetopias jubatus* in Alaska, USA. *Mar. Ecol. Prog. Ser.* 229, 291–312.
- Worthy, G.A.J., 1987. Ecological Energetics of Harp and Gray Seals: Implications From a Simulation Model. In: Huntley, A.C., Costa, D.P., Worthy, G.A.J., Castellini, M.A. (Eds.), *Approaches to marine mammal energetics*. Soc. Mar. Mammal Spec. Publ., 1. Allen Press, Lawrence, KS, pp. 227–246.
- Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. *Analysing Ecological Data*. Springer, New York.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer.
- Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. *Methods Ecol. Evol.* 1, 3–14.
- Zuur, A.F., Hilbe, J.M., Ieno, E.N., 2013. *A Beginner's Guide to GLM and GLMM With R. A Frequentist and Bayesian Perspective for Ecologists*. Highland Statistics. Ltd 256.

## Glossary

- Metabolic rate* ( $\dot{V}O_2$ ): Rate of oxygen consumption per unit of mass, usually expressed in mL O<sub>2</sub> min<sup>-1</sup> kg<sup>-1</sup>.
- Basal metabolic rate (BMR)*: Average metabolic rate of adult animals while at rest in a thermal neutral environment and in a post-absorptive state (Kleiber, 1975).
- Resting metabolic rate (RMR)*: Average metabolic rate of an animal while at rest in a thermal neutral environment and in a post-absorptive state. Minimum values for RMR are often used as estimates of BMR.
- Heat increment of feeding (HIF)*: The increase in metabolic rate that occurs after the ingestion of a meal, which is associated with digestion, assimilation and nutrient interconversion.