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Submerged swimming and resting metabolic rates in Southern sea lions

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ABSTRACT

We measured the metabolic rate of nineteen wild and three captive, trained Southern sea lions (*Otaria flavescens*, Shaw 1800) during three behavioral states: resting in air ($\dot{V}_{O_2, \text{rest air}}$), resting in water ($\dot{V}_{O_2, \text{rest water}}$) and submerged swimming ($\dot{V}_{O_2, \text{sub swim}}$) using open flow respirometry. We then used these values to estimate total cost of transport (COT) and cost per stroke (CPS) during submerged swimming. Wild animals were placed in a metabolic chamber and captive animals were trained to breathe under a plexiglass dome mounted at the end of a pool. General linear modeling was used to determine whether the incidence of each type of response variable (\dot{V}_{O_2} , CPS, COT, swim speed and stroke rate) could be associated with several explanatory variables (sex, age, animal identity, behavioral state, swimming distance and body mass). The overall mean $\dot{V}_{O_2, \text{rest air}}$ was $6.8 \pm 1.1 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ($n=20$ animals; 7 subadult males, 10 sub-adults females, 3 adults females), which was 2.1 times greater than the predicted basal metabolic rate (BMR) for terrestrial mammals of similar size, and neither body mass nor sex had a significant effect. The mean $\dot{V}_{O_2, \text{rest air}}$ when only adults were considered ($6.3 \pm 0.3 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$; $n=3$ females) was similar to the overall value. The mean $\dot{V}_{O_2, \text{rest water}}$ ($9.0 \pm 0.8 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) and the mean $\dot{V}_{O_2, \text{sub swim}}$ ($21.2 \pm 7.4 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) estimated from repeated measurements in two adult females were 2.9 and 6.8 times greater than the predicted BMR, respectively. Both $\dot{V}_{O_2, \text{rest water}}$ and $\dot{V}_{O_2, \text{sub swim}}$ were significantly greater (1.4 and 3.4 times respectively) than the mean $\dot{V}_{O_2, \text{rest air}}$ estimated in this study, when only adults were compared. The mean COT was $0.14 \pm 0.1 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ ($2.6 \pm 1.0 \text{ J kg}^{-1} \text{ m}^{-1}$), and the mean CPS was $0.38 \pm 0.3 \text{ ml O}_2^{-1} \text{ kg}^{-1} \text{ stroke}^{-1}$; none of these values were significantly different among animals.

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1. Introduction

As with all predators, the ability of Southern sea lions (*Otaria flavescens*) to acquire energy for body maintenance, growth and reproduction depends on successful capture of patchily distributed prey. To achieve a positive energy balance, prey energy must exceed the cost of hunting (searching, pursuing and capturing prey) as well as the cost of processing and assimilating food (Williams et al., 2004). With increasing fisheries competition, the quality and quantity of prey available for top predators such as sea lions can be reduced resulting in poor health, reduced body mass, reduced birth rates, and increased mortality (Trites and Donnelly, 2003). This scenario has been suggested as a possible cause, at least in part, for the population decline of Steller sea lions (*Eumetopias jubatus*, Schreber 1776; Calkins and Goodwin, 1988; Rosen and Trites, 2000; Trites and Donnelly,

2003) and could also be contributing to population declines in other pinniped species such as the Southern sea lion.

Southern sea lions, which range and breed throughout the coastal temperate waters of South America, have been heavily exploited, and current numbers represent a small fraction of historical populations. Although this species is legally protected in most South American countries, many populations have never recovered from intense harvesting during the first half of the 20th century. Population trends in the coastal islands of Uruguay, especially Isla de Lobos, which historically represented a major portion of the world population for this species, have shown a steady annual decline of 2–5% over the past few decades (Paez, 2006; Ponce de León, 2000; Ponce de León and Pin, 2006). Although the cause of the decline remains uncertain, it may be the result of competition with expanding local fisheries and reduced prey availability. In addition, this area is also inhabited by sympatric South American fur seals (*Arctocephalus australis*, Zimmermann 1783) that forage on similar prey species and show a steady population increase (Lima and Páez, 1997; Ponce de León et al., 2000). The potential competition between these top predators

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and the increasing fisheries competition could be affecting prey availability and preventing recovery of the Southern sea lion population.

To better understand the foraging strategies of air-breathing animals preying on underwater resources, we need to determine field metabolic rate (FMR, kJ day^{-1}) at sea, prey preference and foraging success (Sparling and Fedak, 2004). Although the energetic cost of foraging in free-ranging marine mammals is difficult to measure, resting, diving and swimming metabolic rates have been measured in several species of pinnipeds (Boyd et al., 1995; Castellini et al., 1992; Costa and Gales, 2003; Costa and Gentry, 1986; Costa et al., 1989a, 1989b; Davis et al., 1985; Feldkamp, 1987a; Fahlman et al., 2008; Hastie et al., 2007; Hindle et al., 2010; Hurley and Costa, 2001; Liao, 1990; Matsuura and Whittow, 1973; Ponganis et al., 1991; Rosen and Trites, 2002; Sparling and Fedak, 2004; Williams, 1999; Williams and Yeates, 2004; Williams et al., 2004, 2007; Young et al., 2011a, 2011b). However, there are no previous measurements of metabolic rates in Southern sea lions. If an at-sea time budget for these behaviors can be determined using animal-borne recorders, then the captive measurements of metabolic rates for different behaviors can be used to estimate FMR. The goal of this study was to measure the metabolic rate in wild and trained Southern sea lions while resting in air, resting in water and submerged swimming, and estimate the cost per stroke (CPS) during submerged swimming, adding valuable information to the estimation of FMR in free-ranging Southern sea lions.

2. Materials and methods

2.1. Metabolic rate measurements

Metabolic rate was estimated by measuring the oxygen consumption of Southern sea lions during three behavioral states: resting in air, resting in water and submerged swimming. Animals were either placed in a wooden metabolic box (for resting in air measurements) or trained to breathe under a plexiglass dome mounted at the surface of the water at the end of a pool (for resting in water and submerged swimming measurements), both connected to an open flow respirometry system (Sable System International, Inc., Henderson, NV, USA). Air was pulled through the metabolic chamber or dome with a Sable Systems Mass Flow pump at an adjustable flow rate that ranged from 250 to 500 l min^{-1} depending on whether the animals were resting or exercising. At these flows, the percentage of oxygen in the chamber or dome 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 rate (\dot{V}_{O_2}) was calculated using equations from Depocas and Hart (1957) and calibrated in triplicate according to Davis et al. (1985) assuming a respiratory quotient of 0.77. Oxygen concentrations observed in the chamber were $99.29 \pm 0.04\%$ and $99.52 \pm 0.02\%$ of the predicted values for N_2 flows of 2 l min^{-1} and 5 l min^{-1} , respectively.

2.2. Metabolic rate while resting in air

We conducted this part of the study in Isla de Lobos ($35^\circ 01' 50'' \text{ S}$, $54^\circ 53' 00'' \text{ W}$), Uruguay, in May 2010. This island is a rookery of ca. 10,000 Southern sea lions and 180,000 South American fur seals (Ponce de León, 2000; Ponce de León and Pin, 2006) and is located along the northern coast of the La Plata River Ecosystem. Measurements were made at the former sealing facility administered by the Uruguay National Direction of Aquatic Resources (DINARA). A permit for this research was issued to D. Rodríguez by the Ministry of Agriculture and Fisheries of Uruguay (Note A/009/2006; DINARA files 1136/2006 and 1378/2008; Ministerial Resolution 001/1383/2007; file 503/2007).

Nineteen Southern sea lions, thirteen females (10 sub-adults and 3 adults; body mass 56.2–145.6 kg) and six sub-adult males (body mass 55.3–145.6 kg), were captured on the rookery and placed in a corral for less than 72 h. To ensure that the animals were healthy, their physical condition was monitored by veterinarians during captivity. Measurements of oxygen consumption while resting in air ($\dot{V}_{\text{O}_2, \text{rest air}}$, $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) were made by placing each animal in a wooden box (2 m long \times 1 m wide \times 1 m high) connected to the open flow respirometry system (see details above). In accordance with Kleiber (1975), resting metabolism was measured in post-absorptive animals while they remained motionless at a thermal neutral air temperature. To ensure post-absorptive conditions, all measurements were made after the animals had been kept in captivity for at least 24 h. Each animal was allowed to rest in the box for 1 h before beginning metabolic measurements. The inside of the box was completely dark, and the animal's behavior was continuously recorded with infrared video cameras mounted at each end. Animals were considered to be in a resting condition when they had spent at least 1 h lying on the floor and almost completely motionless. The average air temperature inside the box was maintained at $22.3 \pm 2.8^\circ \text{C}$ (range 15–25 $^\circ \text{C}$) by adjusting the air flow. This temperature was within the thermal neutral zone described for California sea lions (*Zalophus californianus*, Lesson 1828; Costa and Williams, 1999; Hurley and Costa, 2001; Liwanag et al., 2009). We calculated the mean $\dot{V}_{\text{O}_2, \text{rest air}}$ for all the animals together and for only the three adult females, even though the values were very similar. $\dot{V}_{\text{O}_2, \text{rest air}}$ was reported as both total metabolic rate in $\text{ml O}_2 \text{ min}^{-1}$ and mass specific metabolic rate in $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$.

Each sea lion was kept in the metabolic box for 2–4 h, and the $\dot{V}_{\text{O}_2, \text{rest air}}$ was determined for each animal during a period of at least 5 min (average duration 18.6 ± 11.4 s.d.; range = 5–48 min) of continuous resting behavior and a steady rate of oxygen consumption. Breathing and heart rates were also monitored visually from the video to ensure the animals were not distressed. In addition to the wild sea lions, a similar protocol was used to measure $\dot{V}_{\text{O}_2, \text{rest air}}$ for one trained, sub-adult male sea lion (SL3, 3 years old, body mass 65 kg) at Mundo Marino Aquarium (see description of the facility below). Therefore, complete rest air data set consisted on single measurements in 1 captive and 19 wild sea lions.

2.3. Metabolic rate while resting in water and during submerged swimming

We conducted this part of the study at Mundo Marino Aquarium in San Clemente del Tuyu, Argentina, from June to September of 2006 and 2007. Two adult, female Southern sea lions (SL1, 15 years old, mean mass 98.6 ± 1.3 kg and SL2, 23 years old, mean mass 113.1 ± 2.1 kg) were trained to remain motionless in an upright position while breathing in a plexiglass dome (0.6 m long \times 0.5 m wide \times 0.59 m high) mounted at one end of a pool (43 m long, 5 m wide and 2 m deep) for measurements of oxygen consumption while resting in water ($\dot{V}_{\text{O}_2, \text{rest water}}$, $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$). For estimates of oxygen consumption during submerged swimming ($\dot{V}_{\text{O}_2, \text{sub swim}}$, $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$), the animals were trained to swim in a straight line for 30 m (1 lap), 60 m (2 laps), 90 m (3 laps) or 180 m (6 laps) before surfacing inside the dome and remaining motionless for ca. 15 min. SL1 was able to swim the full 180 m, but SL2 would only swim a maximum distance of 90 m underwater. Swimming multiple lengths of the tank required that the animals decelerate, change direction, and then accelerate at the end of each lap. However, the change in direction occurred in a continuous movement, and at no time did the animals completely stop. Therefore, we did not attempt to correct for deceleration of the animals at the ends of the pool while swimming multiple laps. Stroke rate was determined from video tapes of each experiment, and swim speed was determined as the total distance swum divided by the duration. Although no measurement of blood lactate was made after submerged swimming, all swimming trials were within the animal's estimated aerobic dive limit (ADL) available

for California sea lions (2–3 min, Ponganis et al., 1997). In addition, the maximum submerged duration never exceeded the routine dive duration (ca. 1.5 min) observed for Southern sea lions in the wild (Rodríguez et al., in press, see Discussion), and all swim trails were voluntary.

The experimental protocol consisted of a set of measurements while resting in water and swimming submerged once per day for each of the two trained sea lions. The protocol began with a sea lion moving from its enclosure to the pool and remaining motionless in the water outside the dome for ca. 3 min. Then the animal entered the dome and remained motionless for 7–10 min while oxygen consumption was measured ($\dot{V}_{O_2 \text{ rest water}}$), after which it returned to its enclosure for 5 min. The animal then returned to the pool to swim submerged for a predetermined number of laps and then enter the dome and remain there breathing motionless for 7–10 min while we measured the post-swimming oxygen consumption used to estimate $\dot{V}_{O_2 \text{ sub swim}}$. Afterwards, the animal returned to its enclosure. All measurements were made between late morning and midday (10:00–12:00 local time) under post-absorptive conditions (more than 14 h postprandial), although small amounts of food were given for training purposes during the trials. As the total amount of food was small and the duration of the experimental trials was short (less than 30 min), it was unlikely that the metabolic rate measurements were affected by the heat increment of feeding (HIF, Rosen and Trites, 1997). Mean air temperature was 13.2 ± 2.8 °C (range 8–18 °C), and mean water temperature was 13.7 ± 1.4 °C (range 12–17 °C). All metabolic measurements were made within the thermal neutral zone described for California sea lions (Costa and Williams, 1999; Hurley and Costa, 2001; Liwanag et al., 2009).

Measurements of $\dot{V}_{O_2 \text{ rest water}}$ were the mean value while the animal remained nearly motionless for at least 7–10 min under the dome. $\dot{V}_{O_2 \text{ sub swim}}$ was estimated from the total oxygen consumed during the post-swimming recovery period in excess of that while resting in water (i.e., the oxygen debt) divided by the duration of submerged swimming. Both $\dot{V}_{O_2 \text{ rest water}}$ and $\dot{V}_{O_2 \text{ sub swim}}$ were divided by body mass to calculate mass specific metabolic rates.

2.4. Cost of transport (COT) and cost per stroke (CPS)

The cost of transport (COT), which is defined as the metabolic cost of moving a unit of mass a unit of distance (Schmidt-Nielsen, 1979), was estimated as the mass specific metabolic rate of the active animal divided by the mean speed and expressed in $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ or as $\text{J kg}^{-1} \text{ m}^{-1}$ using the conversion factor of $19.3 \text{ J ml O}_2^{-1}$ and assuming a diet of half protein and half fat. Since COT varies with swim speed (Fish, 2000; Watanabe et al., 2011; Williams, 1999), our calculated COT is for the routine speed chosen by each animal. We calculated the cost per stroke (CPS, in $\text{ml O}_2 \text{ kg}^{-1} \text{ stroke}^{-1}$), which is the oxygen consumed per stroke of the fore flippers, using the equation:

$$\text{CPS} = \left[(\dot{V}_{O_2 \text{ sub swim}} - \dot{V}_{O_2 \text{ rest water}}) \times \text{swim duration} \right] / \text{number of strokes}$$

where $\dot{V}_{O_2 \text{ sub swim}}$ and $\dot{V}_{O_2 \text{ rest water}}$ have the units of $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ and swim duration is in min.

2.5. Statistical analysis

General linear modeling (Montgomery and Peck, 1992; Draper and Smith, 1998) with a Gaussian distribution was used to determine whether the incidence of each type of response variable (\dot{V}_{O_2} , CPS, COT, swim speed and stroke rate) could be associated with several explanatory variables such as sex, age, animal identity, behavioral state, swimming distance and body mass. These explanatory variables were available or not depending on the corresponding data set (rest air, rest water or sub swim). When no other variable was available

(or collinearity was detected), animal identity was used as the putative explanatory variable in the analysis.

Prior to analysis, graphical explanatory techniques were applied to the original data to identify outliers both in the response variable and the explanatory variables. Correlation between explanatory variables (collinearity) was assessed by multiple pair-wise scatter plots (pair plots) and variance inflation factors (VIF) (Montgomery and Peck, 1992; Zuur et al., 2010).

Data for $\dot{V}_{O_2 \text{ sub swim}}$ and $\dot{V}_{O_2 \text{ rest water}}$ consisted of multiple observations from the same two animals, indicating that further extensions were needed. An assumption in regression-type techniques is that the response data are independent, but as the observations are made sequentially over time (e.g., oxygen consumption at time s is likely to depend on that at time $s-1$), the independence assumption was violated. Adding a correlation structure to the data allowing for autocorrelation between the residuals of sequential time units is one way of getting reliable results. Therefore, we applied and compared different correlation structures for irregular temporally correlated data (Schabenberger and Pierce, 2002; Zuur et al., 2009). Optimal models were selected on the basis of the lowest Akaike Information Criterion (AIC) and/or log likelihood ratio test (provided that there were no serious patterns in residuals). When initial analysis indicated violation of homogeneity, a generalized least squares (GLS; Pinheiro and Bates, 2000; Zuur et al., 2009) framework was preferred over linear regression using transformed data because it allows for unequal variance in the variance-covariate terms. 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. All statistical analyses were performed with the software package R (R Development Core Team, 2011). The gls function from the nlme R package (Pinheiro et al., 2011) was used.

3. Results

3.1. Resting in air

Regression analysis of the relationship between total oxygen consumption and body mass could be expressed by equation $\dot{V}_{O_2 \text{ rest air}} = 134.98 + 5.16 \text{ BM}$ ($F_{1,17} = 59.64$; $p < 0.001$; $R^2 = 0.78$) where $\dot{V}_{O_2 \text{ rest air}}$ is in $\text{ml O}_2 \text{ min}^{-1}$ and BM is body mass in kg (Fig. 1). The overall mean mass specific $\dot{V}_{O_2 \text{ rest air}}$ was $6.8 \pm 1.1 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ($n = 20$ animals; range 4.3–9.1) or $20.2 \pm 3.2 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-0.75}$, which was 2.1 times greater than the predicted BMR for terrestrial mammals

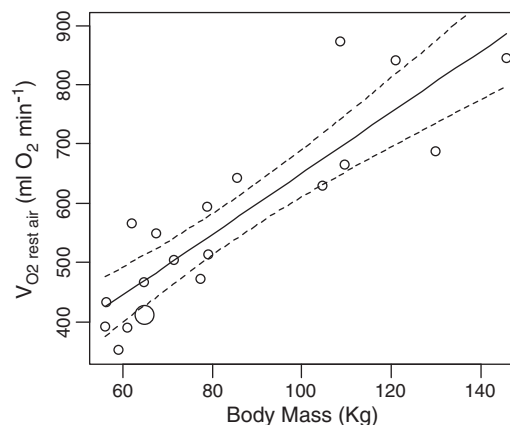


Fig. 1. Estimated metabolic rate while resting in air ($\dot{V}_{O_2 \text{ rest air}}$; in $\text{ml O}_2 \text{ min}^{-1}$) as a function of body mass (kg). Dashed lines are the 95% confidence intervals. The double size point corresponds to the captive trained sea lion (SL3).

of similar size (Kleiber, 1975). As the $\dot{V}_{O_2 \text{ rest air}}$ obtained from the one captive sea lion (SL3; $6.3 \pm 0.3 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) was similar to the values obtained for the wild animals, it was included in the calculation of the overall mean. The mass specific $\dot{V}_{O_2 \text{ rest air}}$ when only adults were considered ($n=3$ animals) was $6.3 \pm 0.3 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$, which was highly consistent with the overall range of values and within the limits of measurement using this technique.

After initial exploration of the data, pair plots and VIFs of the continuous variables indicated strong collinearity between age and body mass for mass specific $\dot{V}_{O_2 \text{ rest air}}$. Therefore, only body mass was used as the putative explanatory variable in this analysis. Neither body mass nor sex had a significant effect on the mass specific $\dot{V}_{O_2 \text{ rest air}}$ ($p>0.05$) suggesting that it was similar over the range of body masses and between males and females.

3.2. Resting in water

The mean $\dot{V}_{O_2 \text{ rest water}}$ was $9.0 \pm 0.8 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ($N=28$ and 20 for SL1 and SL2, respectively; range 7.3 – 10.7) or $28.7 \pm 2.8 \text{ ml O}_2^{-1} \text{ min}^{-1} \text{ kg}^{-0.75}$, which was 2.9 times greater than the predicted BMR for terrestrial mammals of similar size (Kleiber, 1975). When comparing repeated measurements of $\dot{V}_{O_2 \text{ rest air}}$ values for the two animals, AIC and a likelihood ratio test indicated that a model with Spherical correlation (CorSpher) was better than a model without correlation (AIC = 117.11; L-ratio = 5.38, $df=2$, $p<0.01$). However, no significant differences were found using animal identity as a variable ($p>0.05$), which indicated that both animals had similar values for $\dot{V}_{O_2 \text{ rest air}}$. No covariates other than animal identity were measured for $\dot{V}_{O_2 \text{ rest water}}$.

3.3. Submerged swimming

The overall mean $\dot{V}_{O_2 \text{ sub swim}}$ was $21.2 \pm 7.4 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ ($N=28$ and 15 for SL1 and SL2, respectively; range 10.7 – 39.9) or $67.6 \pm 23.7 \text{ ml O}_2^{-1} \text{ min}^{-1} \text{ kg}^{-0.75}$, which was 6.8 times greater than the predicted BMR for terrestrial mammals of similar size (Kleiber, 1975) and 2.3 times greater than the $\dot{V}_{O_2 \text{ rest water}}$ measured in this study. The mean overall COT was $0.14 \pm 0.1 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ (range 0.1 – 0.3) or $2.6 \pm 1.0 \text{ J kg}^{-1} \text{ m}^{-1}$ (range 1.3 – 4.8), and the mean CPS was $0.38 \pm 0.3 \text{ ml O}_2^{-1} \text{ kg}^{-1} \text{ stroke}^{-1}$ (range 0.1 – 1.2).

There were some differences in the submerged swimming ability between the two sea lions. Whereas SL1 was able to swim both 90 and 180 m, SL2 would only swim 60 and 90 m. As a result of these behavioral differences, confounding factors were detected between the variables of animal identity and swimming distance. Therefore, animal identity was selected to rule out differences between the two animals, and data analysis was restricted to those observations for which the animals swam the same distance (90 m). The resulting optimal models explaining $\dot{V}_{O_2 \text{ sub swim}}$, COT and CPS versus animal identity were GLMs without correlation structure. In all three cases, modeling results confirmed that the variable of animal identity was not significantly related to \dot{V}_{O_2} , CPS or COT ($p>0.05$).

Overall mean stroke rate and swim speed (considering all swim distance data) were $37.2 \pm 3.4 \text{ strokes min}^{-1}$ and $2.8 \pm 0.18 \text{ m s}^{-1}$ for SL1, and $27.9 \pm 5.6 \text{ strokes min}^{-1}$ and $2.2 \pm 0.22 \text{ m s}^{-1}$ for SL2. The optimal model describing swim speed as a function of animal identity when equal swim distance was analyzed indicated that a linear model that allowed for unequal variance covariance structure with animal identity was better than a model with equal variances (AIC = -13.79; L-ratio = 5.38, $df=1$, $p<0.01$). Significant differences were found when testing the differences for the variable of animal identity ($p<0.001$), indicating that animal SL1 exhibited a higher average swimming speed than animal SL2. When analyzing stroke rate as a function of animal identity, a linear regression with a GLS extension incorporating a rational quadratic correlation (CorRatio) was better than a model without correlation (AIC = -43.43; L-ratio =

11.07, $df=2$, $p<0.01$), but no significant effect of the covariate animal identity was found in that model.

3.4. Comparison of resting in air, resting in water and submerged swimming

Nominal variables such as type of animal (wild or captive) and behavioral state (rest air, rest water or sub swim) were confounding and thus not considered together in the analysis. For analytical purposes, the variable behavioral state was used as the recognized explanatory variable in the analysis comparing \dot{V}_{O_2} . Adult-females were used for this comparison to prevent highly unbalanced data among behavioral states categories and to strictly conform with Kleiber's conditions for measuring BMR while resting in air. Since no temporal correlation was found among the repeated observations from both animals (see \dot{V}_{O_2} analysis above), a mean value per animal was thus considered as a representative measurement for both submerged swimming and resting in water, and finally added to single observations taken from the wild animals (resting in air). The ANOVA analysis showed that behavioral state had a significant effect on \dot{V}_{O_2} ($F_{2,4}=592.3$, $p<0.001$), indicating that animals resting in water and during submerged swimming had higher mean values of \dot{V}_{O_2} (1.4 and 3.4 times, respectively) compared to resting in air (Fig. 2).

4. Discussion

The present study included the estimation of $\dot{V}_{O_2 \text{ air rest}}$ in both sub-adult and adult Southern sea lions in agreement with Kleiber's (1975) conditions regarding resting motionless, a thermally neutral environment and being post-absorptive. In the case of adults, they also met the fourth condition (age) for estimating the basal metabolic rate (BMR), therefore adult $\dot{V}_{O_2 \text{ air rest}}$ could be useful to be directly compared with BMR estimations in other studies. Despite this distinction, our results show that the $\dot{V}_{O_2 \text{ air rest}}$ of adults was very similar to sub-adults (6.3 ± 0.6 and $6.8 \pm 1.2 \text{ ml O}_2^{-1} \text{ kg}^{-1}$ respectively), and no significant effect of body mass on $\dot{V}_{O_2 \text{ air rest}}$ was observed indicating that the younger animals (>2 years) had achieved an adult metabolic rate. Therefore, we consider our overall $\dot{V}_{O_2 \text{ air rest}}$ value a good estimate of the resting metabolic rate (RMR) for this species, which is probably not too different from the real BMR. Telemetry data from a foraging study of Southern sea lions also suggest comparable physiological abilities between sub-adult and adults, taking into account the similar foraging trip duration, distance travelled and transit speed (Rodríguez et al., in press).

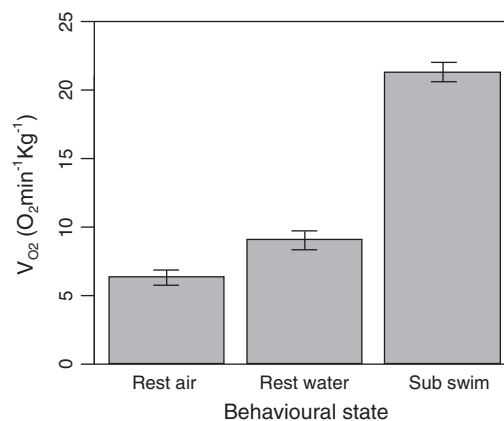


Fig. 2. Fitted values of metabolic rate (\dot{V}_{O_2} , in $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) from the ANOVA model showing the mean and standard errors for the behavioral states of resting in air, resting in water and submerged swimming. Only adult females were used in the model.

The overall mean $\dot{V}_{O_2 \text{ air rest}}$ of $6.8 \pm 1.1 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$ was 2.1 times higher than predicted for terrestrial mammals of equivalent mass (Kleiber, 1975), which is consistent with estimates for other pinnipeds (i.e., 2–3 times greater than predicted; Boyd et al., 1995; Costa et al., 1989a, 1989b; Costa and Gales, 2003; Costa and Gentry, 1986; Davis et al., 1985; Feldkamp, 1987a; Hurley and Costa, 2001; Liao, 1990; Matsuura and Whittow, 1973; Ponganis et al., 1991). The reason for an elevated resting metabolic rate relative to terrestrial mammals has not been determined, but it may be necessary for sea lions and other pinnipeds in order to maintain a constant core body temperature in water, which conducts heat at least 25 times faster than in air (Schmidt-Nielsen, 1979). Similar results have been observed for sea otters (*Enhydra lutris*) which have a resting metabolic rate 2–3 times higher than allometric prediction for a terrestrial mammal of similar size (Miller, 1974; Costa, 1982; Davis et al., 1988; Williams et al., 1988). Although the thermal neutral zone has not been determined for southern sea lions, the lower critical temperature (T_{LC}) for adult California sea lions in water is 6.4°C (Liwanağ et al., 2009), which is much lower than the mean air and water temperatures during the experimental phases of our study and the winter water temperature found in La Plata River estuary ($10\text{--}12^\circ\text{C}$; Guerrero et al., 1997). Therefore, our animals were considered within their thermal neutral zone even though they had a $\dot{V}_{O_2 \text{ air rest}}$ higher than predicted for terrestrial mammals of similar size.

The mean $\dot{V}_{O_2 \text{ rest water}}$ ($9.0 \pm 0.8 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$), although statistically different, was only ca. 30% higher than the $\dot{V}_{O_2 \text{ rest air}}$. The animals resting in water showed some postural movement because they were alert and had to position themselves upright in the dome. Although nearly motionless while in water, they were not recumbent as was the case for animals resting in air. As a result, the increase in energy expenditure while resting beneath the dome might have been caused by positioning themselves upright in the dome than to real differences in RMR between air and water. Therefore, the resting metabolic rate for the sea lions from this study seems to be similar in air and water when the temperature is above the estimated T_{LC} .

The overall mean $\dot{V}_{O_2 \text{ sub swim}}$ ($21.2 \pm 7.4 \text{ ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$) was 2.3 times greater than $\dot{V}_{O_2 \text{ rest water}}$, and 6.8 times greater than the predicted BMR for terrestrial mammals of similar size. Our values and their relation to the predicted BMR were similar to those reported for other sea lions and fur seals. Costa and Gales (2003) found that Australian sea lions (*Neophoca cinerea*, Péron 1816) had at-sea resting and diving metabolic rates 2.3 and 6.2 times greater than the predicted BMR, respectively. Boyd et al. (1995) found that captive California sea lions had resting and maximum submerged swimming metabolic rates 2.3 and 6.8 greater than the predicted BMR, respectively. Costa and Gales (2000) found that New Zealand sea lions (*Phocarctos hookeri*, Peters 1866) had an at-sea, diving metabolic rate 5.8 greater than the predicted BMR. Finally, Costa et al. 1989a reported that Antarctic fur seals (*Arctocephalus gazella*, Peters 1875) had an at-sea metabolic rate that was 6.7 times greater than the predicted BMR. The only study that differs with our results is for Steller sea lions that were trained to swim to depth (between 5 and 30 m) on command and remain stationary at the target light for a predetermined duration (between 60 and 200 s) (Fahlman et al., 2008; Hastie et al., 2007). The results indicated a diving metabolic rate that was not significantly different from resting at the surface (Fahlman et al., 2008) or about 45% lower (Hastie et al., 2007) depending on whether the sea lion or the trainer determined the inter-dive interval. Regardless, most of these dives were spent stationary at the target and are not directly comparable to the continuous, submerged swimming in the current study.

Although we only had two trained sea lions for this study, the mean values for $\dot{V}_{O_2 \text{ rest water}}$ and $\dot{V}_{O_2 \text{ sub swim}}$ (and corresponding estimates of COT and CPS; discussed latter) were not significantly different between animals. In addition, the voluntary submerged swimming durations for our animals were similar to those for wild Southern sea

lions. Based on satellite telemetry, 60% of routine dives for Southern sea lion females from Isla de Lobos were 30–60 s in duration, and 90% were less than 90 s (Rodríguez et al., in press). In addition, most dives (91%) of lactating Southern sea lion females off northern Patagonia were shorter than 4 min (Werner and Campagna, 1995). The sea lions in our study swam faster than the average speeds ($0.9\text{--}1.9 \text{ m s}^{-1}$) during diving recorded for a variety of wild sea lions and fur seals ranging in body mass from 27 to 137 kg (Ponganis et al., 1990). However, swim speed measurements in the later study probably involved periods of gliding or reduced speed while foraging, whereas our captive sea lions were swimming continuously in a horizontal position. Therefore, we think our estimates of $\dot{V}_{O_2 \text{ rest water}}$ and $\dot{V}_{O_2 \text{ sub swim}}$ are good estimates of resting and swimming (i.e., active stroking) metabolic rates.

In contrast, the swimming and diving metabolic rates reported for seals are often less than for sea lions and fur seals (Sparling and Fedak, 2004; Williams et al., 2004; Castellini et al., 1992; Davis et al., 1985). This difference may result from several factors, but the routine swim speeds of sea lions and fur seals are probably much faster than for seals. Since locomotory power is proportional to (velocity)³, the metabolic cost for higher speed swimming increases rapidly (Davis and Weihs, 2007). A biomechanical model developed with the largest dataset available of free-ranging diving animals (sea birds, marine mammal and turtles) suggested that metabolic power production is limited by swim speed (Watanabe et al., 2011). Hence, higher routine swim speeds may account for much of the apparent difference in swimming and diving metabolic rates for seals and sea lion-fur seals.

As most measurements of metabolic rates in both seals and sea lion-fur seals during submerged swimming have been made in captivity and usually involved horizontal swimming (continuous stroking or stroke-and-glide) in a pool or water flume or trained to make shallow dives and station on a target (Fahlman et al., 2008; Hastie et al., 2007), direct comparison with freely diving metabolic rates should be made with caution. Free-ranging marine mammals use cost efficient modes of locomotion (stroke-and-glide and extended periods of gliding) while diving, especially during descent (Davis and Weihs, 2007; Madden et al., 2008; Williams et al., 2000), which are difficult to simulate in captive marine mammals.

The mean COT ($0.14 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$; $2.6 \text{ J kg}^{-1} \text{ m}^{-1}$) for the two sea lions in our study was nearly identical to that for smaller (23 kg), subadult California sea lions ($0.12 \text{ ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$) (Feldkamp, 1987a) but less than for subadult Steller sea lions ($4.4 \text{ J kg}^{-1} \text{ m}^{-1}$) in a swim flume (Rosen and Trites, 2002). In addition, our value was similar (1.4 times higher) to the predicted value obtained from the allometric equation ($\text{COT} = 7.79 \text{ mass}^{-0.29}$) calculated by Williams (1999) for a variety of marine mammals ranging in size from 21 to 15,000 kg and highly similar (1.1 times higher) to the predicted value from the allometric equation ($\text{COT} = 7.01 \text{ mass}^{-0.205}$) of Culik et al. (1994) for pinnipeds and bottlenose dolphins. Our results agree with the conclusion of Williams (1999) that pinnipeds and cetaceans have converged on an energetic optimum even though these species use different modes of locomotion.

Although Feldkamp (1987a, 1987b) did not determine the cost per stroke (CPS) for captive, subadult California sea lions (mean body mass 30.4 kg) swimming in a water flume, we estimated CPS based on his published results to be $0.33 \text{ ml O}_2 \text{ kg}^{-1} \text{ stroke}^{-1}$ at a swim speed of 1.8 m s^{-1} , which was the speed at minimum COT and a flipper stroke frequency of 25 strokes min^{-1} . This estimated CPS is very similar to the value obtained during this study ($0.38 \text{ ml O}_2 \text{ kg}^{-1} \text{ stroke}^{-1}$). The only other pinniped species for which CPS has been measured is the Weddell seal. Williams et al. (2004) calculated the CPS of voluntary diving Weddell seals to be $0.119 \text{ ml O}_2 \text{ kg}^{-1} \text{ stroke}^{-1}$, which is 69% less than the value for sea lions in our study. However, Williams defined a stroke as one lateral motion of the hind flippers to the right or left, not a complete stroke cycle as was the case in our study.

Therefore, the cost of one stroke cycle for a Weddell seal would be $0.238 \text{ ml O}_2 \text{ kg}^{-1} \text{ stroke}^{-1}$, which is still 38% less than our value. The difference may result from the mode of locomotion (fore flipper propulsion) used by sea lions in which thrust is generated by both flippers throughout the stroke cycle (Feldkamp, 1987b), as opposed to the hind flipper propulsion of Weddell seals in which each flipper alternately generates thrust for only half of the stroke cycle, then collapses during the other half of the cycle. In addition, sea lions (and fur seals) are simultaneously using two propulsive surfaces (fore flippers) throughout the complete stroke cycle compared to alternating propulsive surfaces (hind flippers) used by seals, and this may partly explain the higher CPS. Although the CPS for sea lions appears to be higher than for seals, the predicted COT is similar (Culik et al., 1994; Williams, 1999). This implies that sea lions stroke less frequently than seals while swimming at a speed that gives the minimum COT.

This study was the first attempt to determine the CPS for sea lions. The value is useful because it enables energetic costs to be assessed for free-ranging animals in which direct measurements are difficult, and avoids the potential problems associated with using doubly labeled water or swimming speed as predictors for metabolism. Recent technologies have made possible to record data on diving and swimming performance (total duration, effective stroke rate and gliding time during ascent, bottom and descent periods) and resting behavior at-sea with animal borne instruments (Davis et al., 1999, 2001, 2003, 2004; Sato et al., 2002; Fuiman et al., 2007; Madden et al., 2008; Williams et al., 2000). The combination of this information with our results (CPS during submerged swimming and RMR) will enable us to estimate submerged swimming and resting energy metabolism at-sea, adding valuable information to the estimation of total field metabolic rate (FMR) for free-ranging Southern sea lions. Since Southern sea lions are shallow, benthic divers (Werner and Campagna, 1995; Thompson et al., 1998) with 74% of the time at depth in waters below 10 m (Rodríguez, unpublished data), we believe that metabolic measurements of submerged swimming could be a good approximation for models of FMR in this species. In addition, video recorded prey capture (species, number and size) can be used to estimate overall energy intake during diving that will enable us to develop energetic models of foraging effort, prey preference and foraging efficiency. This information will be useful for understanding the ecology of the declining stock of Southern sea lions inhabiting the La Plata River Ecosystem. A better knowledge of the energetic cost of foraging will help in better identifying the principal causes of the recent declines in abundance and developing management policies for fisheries that will contribute to better conservation policies.

Abbreviations

BMR	basal metabolic rate
COT	cost of transport
CPS	cost per stroke
FMR	field metabolic rate
$\dot{V}_{\text{O}_2 \text{ rest air}}$	resting in air metabolic rate
$\dot{V}_{\text{O}_2 \text{ rest water}}$	resting in water metabolic rate
$\dot{V}_{\text{O}_2 \text{ sub swim}}$	submerge swimming metabolic rate

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Glossary

- Metabolic rate** (\dot{V}_{O_2}): Rate of energy utilization or amount of energy used per unit of time and per unit of mass, usually expressed in $\text{ml O}_2 \text{ min}^{-1} \text{ kg}^{-1}$.
- Field metabolic rate (FMR)**: Average rate of energy utilization (or the average metabolic rate) as the animal goes about its normal activities on its natural environment.
- Basal metabolic rate (BMR)**: Average rate of energy utilized by adult organisms while at rest in a thermal neutral environment and in a post-absorptive state (Kleiber, 1975).
- Cost of transport (COT)**: Metabolic cost of moving a unit of mass a unit of distance, usually expressed in $\text{ml O}_2 \text{ kg}^{-1} \text{ m}^{-1}$ or $\text{J kg}^{-1} \text{ m}^{-1}$ (Schmidt-Nielsen, 1979).
- Cost per stroke (CPS)**: Amount of oxygen consumed by a unit of mass per stroke during active stroking locomotion, usually expressed in $\text{ml O}_2 \text{ kg}^{-1} \text{ stroke}^{-1}$. In the case of this study, each stroke is considered as a complete cycle movement of the fore flippers.