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Basal metabolism of an adult male killer whale (*Orcinus orca*)

GRAHAM A. J. WORTHY,^{1, 2} TAMARA A. M. WORTHY, and PAMELA K. YOCHEM, Hubbs-SeaWorld Research Institute, San Diego, California 92109, U.S.A.; CHRISTOPHER DOLD, SeaWorld Parks and Entertainment, Orlando, Florida 32821, U.S.A.

Knowing how much energy an individual requires is fundamental to resolving a number of questions about the role an animal plays in its ecosystem. Various authors have used different approaches to assess energy needs of *in situ* (free-ranging) killer whales (*Orcinus orca*), including estimates based on observations of prey capture and consumption rates (e.g., Williams *et al.* 2004, Maniscalco *et al.* 2007) or extrapolations from bioenergetic models using data derived from *ex situ* (managed in zoological parks) individuals (e.g., Kastelein and Vaughan 1989, Kasting *et al.* 1989, Kriete 1995, Kastelein *et al.* 2003). The few measurements that have been made on *ex situ* killer whales include assessments of respiratory capabilities (e.g., Spencer *et al.* 1967, Kriete 1995), quantification of food/energy intake rates (e.g., Kastelein and Vaughan 1989, Kastelein *et al.* 2000a), or measures of metabolic rate (e.g., Kasting *et al.* 1989, Kriete 1995). These latter measurements have frequently not met the criteria of Kleiber (1975) due to whales being immature, pregnant, and/or active. The goals of the present study were to develop a functional methodology that could be employed to measure resting oxygen consumption rates of *ex situ* killer whales and obtain basal metabolic rate (BMR) measurements.

The foundation of any bioenergetic model is an accurate assessment of BMR. They are not only used to estimate “resting” costs, but multiples of BMR are often used to estimate total field metabolic rates. Such models are important for estimating energy expenditures since it is difficult or impossible to acquire direct measures, especially for *in situ* whales, due to their large size and limited accessibility. Mass-balance simulation models have been used to estimate feeding requirements for some marine mammal species (e.g., Winship *et al.* 2002, Williams and Noren 2009), but because actual energetic measurements (including critical estimates of BMR) are impossible

¹Corresponding author: (e-mail: graham.worthy@ucf.edu).

²Current address: Department of Biology, University of Central Florida, 4000 Central Florida Blvd., Bldg. 20, Orlando, FL 32816-2368.

to collect in the field, these models are based on published allometric relationships and limited available empirical data. Despite these limitations they are the only practical solution to estimating energetic requirements of large, highly mobile marine mammals.

BMR is the maintenance operating metabolism of an organism, *i.e.*, the metabolic requirement which is needed to sustain life processes of an animal in a resting state. Kleiber (1975) emphasized that BMR determinations must meet four criteria. Only those metabolic rates measured on mature (nonpregnant) animals, within their thermoneutral zone, in the postabsorptive state, and while resting are acceptable as measures of basal metabolism. The violation of any of these conditions can result in a doubling or tripling of metabolic rate (see Gallivan 1992, Speakman *et al.* 1993). Over the years there has been considerable debate as to whether cetaceans, and indeed marine mammals in general, have elevated metabolic rates compared to terrestrial species. Sea otters, otariids, and small odontocetes seem to have elevated metabolisms, perhaps double what is predicted for a similar-sized terrestrial mammal (*e.g.*, Kanwisher and Sundnes 1966, Kasting *et al.* 1989, Noren 2011). However, basal metabolic rates of phocid seals seem to be consistent with Kleiber (1975) and many authors (*e.g.*, Lavigne *et al.* 1986, Worthy 1987, Worthy *et al.* 1987, Innes and Lavigne 1991, Speakman *et al.* 1993, Otani *et al.* 2001, Williams *et al.* 2001, Rosen and Trites 2013) have suggested that, when marine mammals are measured following the conditions of Kleiber (1975), their metabolic rates do not differ significantly from terrestrial mammals.

Most direct assessments of metabolism in cetaceans have focused on smaller species, with a number of studies examining basal metabolism (*e.g.*, Yazdi *et al.* 1999, Williams *et al.* 2001) and thermoregulatory capabilities (*e.g.*, Williams *et al.* 1999, Williams *et al.* 2001, Meagher *et al.* 2002) of bottlenose dolphins (*Tursiops truncatus*). Direct measures of BMR have been undertaken on other small cetaceans such as harbor porpoises (*Phocoena phocoena*) (*e.g.*, Kanwisher and Sundnes 1966, Worthy *et al.* 1987, Reed *et al.* 2000), Hawaiian spinner dolphins (*Stenella longirostris*) (*e.g.*, Hampton and Whittow 1976), and Pacific white-sided dolphins (*Lagenorhynchus obliquidens*) (*e.g.*, Rechsteiner *et al.* 2013). Relatively few direct measurements of BMR have been undertaken on larger cetaceans, and are limited to beluga whales (*Delphinapterus leucas*) (*e.g.*, Kasting *et al.* 1989, Godfrey 2009, Rosen and Trites 2013) and false killer whales (*Pseudorca crassidens*) (*e.g.*, Kastelein *et al.* 2000b). Studies on larger cetaceans, such as gray whales (*Eschrichtius robustus*) and minke whales (*Balaenoptera acutorostrata*) have variously measured respiratory rates of *in situ* animals, measured oxygen consumption in *ex situ* juveniles, or measured tidal lung volume to estimate metabolic rates (*e.g.*, Wahrenbrock *et al.* 1974; Kooyman *et al.* 1975; Sumich 1983, 1994, 2001; Folkow and Blix 1992; Sumich and May 2009). As a result of the paucity of data on larger species, researchers have used estimates of metabolic rate extrapolated from smaller species, to calculate energetic requirements (*e.g.*, Sumich 1983, Lavigne *et al.* 1990, Gala-Hernandez *et al.* 2008, Williams and Noren 2009, Noren 2011).

There are limited measures of resting metabolism of killer whales available (*e.g.*, Kasting *et al.* 1989, Kriete 1995) and both of these previous studies include data collected from actively swimming whales, thereby violating Kleiber's (1975) criteria for resting metabolism. In the present study, we measured BMR of an *ex situ* adult male killer whale (5,318 kg), estimated to be 27 yr of age. We combined this value with measured daily activity budgets, and compared it to food intake rates thereby allowing us to compare measured BMR with independent assessments of energy intake and expenditures.

The whale in the present study had been conditioned to rest underneath a flow-through metabolic dome by behavioral training staff starting 3 mo prior to actual measurements. For metabolic rate trials, the whale was fasted overnight and was stationed near the side of the pool for 20–30 min prior to a measurement period. The whale floated horizontally for all measurements. During the approximately 15–30 min measurement period, a hood (75 cm × 75 cm × 120 cm high, volume 675 L) was suspended over the whale's blowhole, in contact with its back, such that exhaled air could not escape the system. This hood, with a frame constructed of 1 in. PVC pipe, was covered with transparent flexible plastic film (Glass-Gard, Solamatrix Inc, St. Petersburg, FL) and had foam pipe wrap around the base. The 12 mm thick film was composed of two ultra-thin plies of polyester laminated to one another with a durable adhesive to form what appears to be a single sheet. One of the plies has a micro-thin layer of metal imbedded into it which is securely trapped between the plies after lamination. This material is virtually impervious to gas transfer. Air entered through gaps around the base of the hood and exited *via* a 15 cm diameter opening at the top of the hood. The hood captured normal resting exhalations, but could not completely trap some infrequent forceful exhalations and these latter periods were excluded from further analyses. A Sable Systems (Sable Systems International, Las Vegas, NV) open-flow respirometry system, FC-1B oxygen analyzer, CA-2A CO₂ analyzer, PC-3 condensing dryer with a 500H Flow Kit mass controller and pump (STP corrected) was used to measure oxygen consumption rate. A Universal Interface (UI-2) was used to convert the analog data to a digital signal for laptop recording using Sable Systems ExpeData v. 2.0. Negative system pressure was maintained at all times (except for the aforementioned forceful exhalations) with air being pulled through the hood at 500 ± 15 L/min. A subsample of this main airstream was removed, dried, and pushed through the gas analyzers at 250 ± 2 mL/min. Excurrent O₂ and CO₂ concentrations (%), flow rate (L/min), air temperature (°C) and barometric pressure (kPa) were sampled every second and recorded. The system was conditioned, and baseline measurements recorded, for a minimum of 20 min prior to sessions. Gas analyzers were calibrated off-site with gases of known composition on a daily basis. O₂ and CO₂ meters were zeroed using 100% dry nitrogen, CO₂ meter span was set using 1.0% CO₂ (99.0% N₂), and the O₂ meter was set to 20.94% (outdoors) using soda lime to remove CO₂ and the PC-4 sample dryer to remove water vapor. The entire system was validated with N₂ gas according to Fedak *et al.* (1981) where flow rate of N₂ (±1.5%) into the dome was monitored using an electronic flow meter (Model #1826; Omega Engineering Inc., Stamford, CT).

In order to attain a steady rate of O₂ consumption a minimum of 5 min of normal breathing was required prior to any experimental measurements. Measurement periods lasted for 15–30 min during each session, with a total of four sessions ultimately being measured. Oxygen consumption and carbon dioxide production rates were calculated using Sable Systems ExpeData software ver. 2.0. Rates of oxygen consumption (VO₂) and carbon dioxide production (VCO₂) (corrected for STPD) were calculated using equations 10.6 and 10.7 from Lighton (2008). Values used in the estimation of BMR consisted of the mean oxygen consumption rate for the most consistently stable portion of the sampling period (minimum of 15 min) for each measurement period. Oxygen consumption rates were converted to energy using the conversion factor of 20.1 kJ/L O₂ consumed.

Basal metabolic rate (BMR) measurements were made while the whale was awake, resting, and in a postabsorptive state, with water temperature within the whale's presumed thermoneutral zone (13°C). The whale exhibited a basal metabolic rate of

2,274.9 ± 148.1 W (196.6 MJ/d) ($n = 4$), comparable to that predicted by Kleiber (1975) (1.1 ± 0.1 times predicted) for an average adult terrestrial mammal of similar size (2,117 W) (Table 1, Fig. 1).

Activity budget data was obtained by animal care staff observing the animal continuously (24 h/d) for a period of seven consecutive days, during which time durations of different behavioral states were monitored and recorded. These behavioral states consisted of resting (<1.0 m/s), slow speed swimming (1.0 m/s), moderate swimming (2.0 m/s), and active swimming/performing (3.0 m/s) and were collectively used to generate a time-activity budget that could be compared to food intake as an independent assessment of metabolic expenditure. On average the whale spent 69.6% (16.7 h) of the day resting, 13.3% (3.2 h) of the day undertaking slow speed swimming (1.0 m/s), 12.5% (3.0 h) of the day doing moderate swimming (2.0 m/s), and 4.5% (1.1 h) active swimming and/or performing similar to adult *ex situ* killer whales in Kriete (1995). Using a linear regression of Kriete's (1995) data on cost of swimming, in conjunction with our activity budget data, resulted in an estimated daily energy expenditure of 358 MJ/d (equations and results in Table 2).

Over a 1 mo period, concurrent with metabolic rate measurements, the whale received an average of 91 kg/d of herring (*Clupea borealis*) and capelin (*Mallotus villosus*) with an energy density of 5.3 MJ/kg, equating to a daily gross energy intake of 482.3 MJ. Assuming an average assimilation efficiency of 90% and urinary energy losses of 10% (Worthy 2001, Williams *et al.* 2004), this equates to approximately 391 MJ/d of energy available to meet metabolic demands. Estimated daily metabolic expenditures from the activity budget and energy intake data both independently equal approximately two times our measured BMR.

The results of the present study confirm that it is feasible to collect data on basal metabolic rates from large cetaceans in zoological parks using indirect calorimetry. The system that was developed for the present study proved to be portable and effective, and was readily and rapidly accepted by the animal. Our results are also consistent with the hypothesis that adult killer whales have a basal metabolic rate consistent with predicted values for an adult terrestrial mammal of comparable mass (Kleiber 1975). However, since these data relate to only a single *ex situ* adult whale, where a variety of factors may influence metabolic rate, caution must be exercised when extrapolating to *in situ* whales. Rates measured in the present study were lower than those previously collected from killer whales that were not resting, were pregnant and/or were not adults (Kasting *et al.* 1989). Consistent with our results, Kriete (1995) measured BMR of two *ex situ* adult killer whales (20 and 21 yr old) and found resting metabolic rates of 1.2–1.3 times that predicted by Kleiber (1975). She also

Table 1. Measured oxygen consumption rates and BMR for a 27-yr-old male killer whale (mass = 5,318 kg) under resting conditions. Predicted basal metabolic rate was 2117.3 W (Kleiber 1975). Mean water temperature was 13°C.

Oxygen consumption (L/min)	BMR (W)	Multiple of Kleiber	RQ
6.0	2,158.6	1.0	0.79
6.3	2,215.7	1.0	0.81
6.8	2,491.9	1.2	0.80
6.3	2,233.5	1.1	0.78
Mean	2,274.9 ± 148.1	1.1 ± 0.1	0.79 ± 0.01

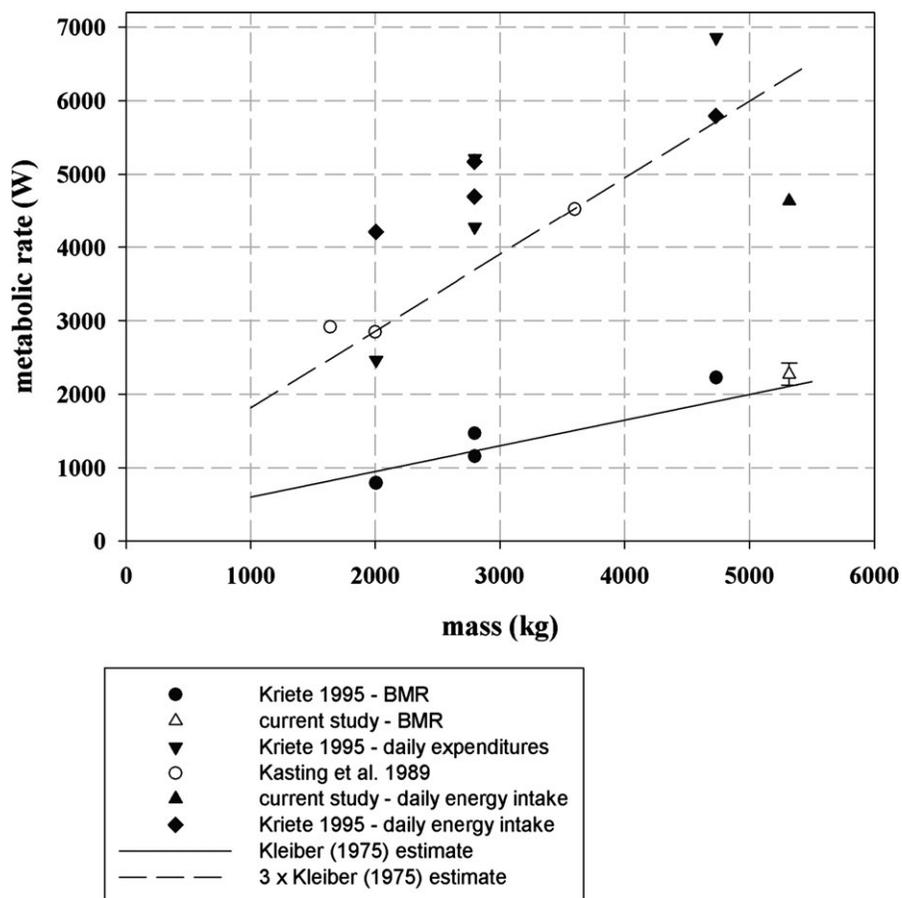


Figure 1. Metabolic rate estimates (basal metabolic rate [BMR] and total daily expenditures) for juvenile and adult killer whales (Kasting *et al.* 1989, Kriete 1995), as well as BMR measurements and estimated daily expenditures (calculated using published digestive efficiencies and measured food intake) collected for the adult whale in the present study. Lines indicating one and three times the predicted BMR are shown for reference (Kleiber 1975).

measured metabolic rates of two younger, but mature, animals (both 11 yr old) and determined resting rates of 0.9 and 1.3 times Kleiber's (1975) predicted value (Fig. 1). Kriete (1995) could only estimate the mass of her whales based on a published mass-length relationship (Bigg and Wolman 1975) to which she applied a 25% mass correction factor derived from other *ex situ* whales (Kriete 1995). Applying this same mass-length relationship (Bigg and Wolman 1975) to the measured length of the whale in the present study, resulted in an estimated mass of 4,303 kg compared to the measured value of 5,318 kg—a 24% difference similar to Kriete's (1995) correction factor.

In the absence of direct measurements of food intake rates in the wild, almost all calculations are based on estimated field metabolic rates (FMR), which in turn are derived from estimated resting metabolic rates, an assessment of whether an animal is

Table 2. Average daily metabolic expenditure was calculated by utilizing an average daily activity budget (see text) with estimated metabolic costs for different swimming speeds (derived from Kriete 1995) and summed over the course of a day. Estimated available net energy from food consumption (see text) is similar to these calculated energy requirements and both are approximately equivalent to two times Kleiber's (1975) predicted basal metabolic rate.

Activity state	Fraction of day (%)	Time (h)	Energy expended ^a (MJ/h)	Energy expended (MJ/d)
Resting, <1.0 m/s	69.6	16.7	8.0	133.6
Slow cruising, 1.0 m/s	13.3	3.2	21.5	68.6
Active swimming, 2.0 m/s	12.5	3.0	34.7	104.1
Performing/training, 3.0 m/s	4.5	1.1	47.8	51.6
Total energy budget	100.0	24		358.0

^aEstimated rates of energy expenditure are derived from the linear relationship between metabolic rate and swimming speed where $MR \text{ (kcal/kg d)} = 14.1 * V + 9.1$ ($R^2 = 0.747$, $F_{1,28} = 79.64$, $P < 0.001$) (from Kriete 1995) (subsequently converted to MJ/h assuming a mass of 5,318 kg).

within its thermoneutral zone, and an estimated cost of locomotion (frequently as a multiple of BMR). This FMR value is then converted to biomass intake using the estimated digestive efficiency and energy density of likely prey. Therefore, the impact of inaccurate measures of BMR can have significant effects on potential estimates of food requirements and hence ecological impact of predator populations. Generally mammalian FMR are in the range of 2–3 times BMR (e.g., Speakman *et al.* 1993) and many authors have estimated the metabolic needs of free-ranging cetaceans as falling in this range when estimating prey consumption and annual energy budgets of larger cetaceans (e.g., Kenney *et al.* 1997, Laidre *et al.* 2004, Leaper and Lavigne 2007, Lockyer 2007, Barlow *et al.* 2008).

In theory, measuring the rate of resting oxygen consumption should be relatively straightforward, but few measurements have ever been made for large *ex situ* cetaceans due to logistical constraints on animal access, equipment needs, and the ability to ensure that measurements are made from resting individuals. Small behavioral state changes, recent feeding, or swimming activity can have major effects on metabolic rate and, therefore, removal of these factors through thorough acclimation and training is critical to the measurement of BMR (Lavigne *et al.* 1986). Recent studies on belugas (Godfrey 2009, Rosen and Trites 2013), where adherence to the criteria of Kleiber (1975) and where adequate training was employed, have measured metabolic rates that were lower than previous studies which did not meet those conditions (*i.e.*, Kasting *et al.* 1989). The present study describes a methodology that can be applied to *ex situ* cetaceans to expand the available database for BMR data and presents metabolic rate values for the largest individual odontocete measured thus far thereby expanding the database for approximating energy requirements for *in situ* killer whales. The results of the present study are not consistent with suggestions that odontocetes have elevated basal metabolic rates, but instead lends cautious support to the notion that at least some species may have BMRs similar to terrestrial mammals of comparable size.

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