**Title**

Bioenergetics of marine mammals: the influence of body size, reproductive status, locomotion and phylogeny on metabolism

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# Bioenergetics of marine mammals: the influence of body size, reproductive status, locomotion and phylogeny on metabolism

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by

**Jennifer L. Maresh**

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# Abstract

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by

Jennifer L. Maresh

Metabolic energy demand is both a cause and consequence of how animals interact with their environments. Describing patterns of metabolism and understanding the drivers underscoring those patterns have been long-standing goals of biology for almost a century. Mammals are often the subject of comparative metabolism studies, and it is clear that their metabolic rates are determined by a complex interaction between a host of morphological, ecological, behavioral and evolutionary factors. In contrast, metabolism is often considered to be less complex for marine mammals, that is, uniformly high across all groups. This perception is the result of a paradigm that took root when determinations on marine mammals were relatively rare, and it has persisted despite a growing number of studies reporting low to moderate metabolic rates in some species.

In the following chapters, I describe the foraging energetics of free-swimming northern elephant seals (*Mirounga angustirostris*) and show that these seals have extremely low field metabolic rates (FMRs) that do not conform to traditional expectations for marine mammals. I also demonstrate the effects of body size and reproductive status on the bioenergetics of this

species, showing that larger, fatter, pregnant seals have lower FMRs and higher foraging success. I also am able to demonstrate the importance of locomotory efficiency in maintaining a low FMR: seals responded to artificially increased locomotion costs by increasing their swimming efforts, thereby increasing FMR and lowering foraging success. These results demonstrate the sensitivity of elephant seals to anthropogenic disturbance in important foraging grounds, and potentially along migration corridors.

These results also demonstrate an energy economy strategy in a species that, by virtue of its shared environment with other marine mammals, would traditionally be predicted to have an elevated metabolic rate. In my last data chapter, I revisit the paradigm underscoring these traditional predictions. I synthesize all mammalian metabolic determinations published to-date and am able to show that the metabolic rates of marine mammals are comparable to those of terrestrial mammals, particularly when they are compared to other carnivores. I also discuss the importance of differences between the various marine mammal groups in their ecologies, behaviors and evolutionary histories in determining metabolic energy demand. These results suggest that metabolism in marine mammals is as complex as in other mammals, and that the assumption of one uniform, high-energy group is not supported by the data. This has important implications for managers interested in predicting the prey requirements of these upper trophic level predators, as traditional models are likely to exaggerate the impact of many species on their environments.

To

my mother, Kate

my sisters, Amie and Destiny

my cousin, Becky

my aunt, Goldie

and my niece, Melody

This work is dedicated to you, the women in my life

who are fighters

who are supporters

who love unconditionally

and who mean everything.

And to the memory of my grandmother, Ruth,

who, I am told, loved seals and whales and wanted to be a marine biologist

...is this a coincidence or what?

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Deciding when a thesis is finished is an exercise in deciding how many cliffhanger endings one can live with, as my work left me with more questions than answers. Which is why I would first like to thank my good friend (and new father) Dai Shizuka, who told me that a thesis is never "done;" that there is always more to do; that a thesis, like any scientific endeavor, is a work in progress, and manuscripts are therefore progress reports. This is a concept with which perfectionist nerd-types like me struggle, but once embraced, opens up the way for the heretofore all-elusive FUTURE RESEARCH DIRECTIONS that determine the kind of scientist one will be...and also conveniently help a lot with research statements and job applications.

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# Chapter 1

# Introduction

## 1.1 Broad context

Metabolic energy fuels living processes at every level of biological organization, making the chemical energy released during the catabolism of food one of the most important resource requirements of organisms (Nagy, 2005). Thus, understanding metabolic energy demand is of fundamental importance to many groups: physiologists are interested in understanding how organisms have adapted to particular environments; ecologists are interested in understanding the role different types of organisms play in their ecosystems; and managers are interested in understanding the basic resource requirements for successful recovery of depleted, and protection of intact, populations. However, organisms differ considerably in their energy needs and, by extension, in their metabolic rates, which are ultimately determined by a complex interaction between an organism's body size, age, phylogenetic history, reproductive status, foraging strategy, diet, activity level, locomotory mode, physical environment, and a multitude of other factors (Nagy et al., 1999; Lovegrove, 2000; McNab, 2000).

The majority of synthesis studies seeking to unravel this complex interaction and determine the most important factors influencing metabolic rate focus on mammals, and they often simplify the issue by dealing with marine mammals in one of two ways: by (1) considering them as one homogenous group by virtue of the physical characteristics of their shared, aquatic environment (e.g., Sibly and Brown, 2007; Speakman and Król, 2010); or (2) excluding them from analyses altogether (e.g., Carbone et al., 2007; White et al., 2009). Both approaches are understandable as the difficulties inherent in obtaining empirical measurements of metabolic rate in far-ranging, large-bodied marine mammals are often insurmountable, and thus relatively few reliable data points exist for marine mammals. However, both approaches are problematic. First, marine mammals are as diverse in their metabolism-influencing traits as are terrestrial mammals, rendering one catchall grouping for 125+ aquatic species questionable. Second, exclusion of marine mammals from comparative analyses excludes an interesting and important group of high-level predators from the collective understanding of how animals work. Given the high trophic position of most marine mammals, understanding their resource requirements is central to quantifying their impacts on prey resources and marine ecosystems (Beverton, 1985; Trites et al., 1997; Boyd, 2002), as well as in predicting the potentially disproportionate impacts of human activities and global climate change on them (Boyd et al., 2008; Baum and Worm, 2009; Estes et al., 2011).

## 1.2 Dissertation outline

Our current understanding of metabolic energy demand in marine mammals, while limited, is nonetheless dominated by the prevailing hypothesis that all species have elevated field metabolic rates (FMRs) and, therefore, high prey intake rates (McNab, 1986a; Speakman and Król, 2010). In the next three chapters (2-4), I present evidence suggesting that this paradigm is no longer viable. I argue instead that FMR in marine mammals varies between species; that it is an emergent property of the same set of complex rules determining FMR in terrestrial mammals; and that perceptions of otherwise are based on sampling bias towards smaller, high-energy species that traditionally have been more tractable for metabolic studies. Recent advances in tagging technology – some of which have been pioneered by my own dissertation committee members – have improved the tractability of some of the more cryptic species, increasing our ability to measure FMR in wild, free-swimming animals. These technological advances allow us to not only answer some of the most fundamental questions regarding the basic resource needs of marine mammals, but also to begin asking new questions about how human-caused disturbances at sea might affect foraging success in these species.

In the first two data chapters (2 & 3), I use the northern elephant seal (*Mirounga angustirostris*) as a case study in the bioenergetics of successful foraging in marine mammals. In **Chapter 2**, I employ a double translocation experiment to obtain empirical measurements of locomotion costs in free-swimming seals and determine FMR in two age classes. I show that northern elephant seals have low at-sea FMRs that decrease with age as seals mature physiologically and growth rates slow. I also experimentally elevate locomotion costs by increasing hydrodynamic drag, causing observable changes in some swimming behaviors and substantial increases in FMR. The results of this chapter demonstrate the vulnerability of elephant seals to disturbance while also providing the information on locomotion costs necessary for construction of energy budgets in migrating seals (Chapter 3).

In **Chapter 3**, I apply the energy cost per flipper stroke determined in the translocation study to the diving records of 20 adult female northern elephant seals during their 2- and 7-month-long foraging migrations. I combine these estimates of energy expenditure with measurements of energy intake (mass gain) to estimate the overall energy budget of each seal, and compare these data to those from three seals with experimentally-increased locomotion costs. I show that, as was the case during the more contrived translocation scenario, migrating elephant seals have very low at-sea FMRs that are easily upset by increased locomotion costs. I also demonstrate the effects of reproductive status and time at sea on FMR, with the interesting result that during the longer migration, pregnant seals have FMRs below predictions of basal rates. The results of this chapter suggest that foraging success in this species depends on minimizing locomotion costs, which aids in maintaining a relatively low metabolic rate, and that this effect is more pronounced during pregnancy. These results also provide empirical support for rejection of the prevailing hypothesis that elevated metabolic rates are a shared characteristic of all marine mammals (Chapter 4).

In **Chapter 4**, I examine and challenge the scientific consensus regarding elevated prey-energy requirements in marine mammals by synthesizing all data published to-date on both basal and field metabolic rates in eutherian mammals. I show that even when measurements are filtered to include only those collected while conforming to established methodological standards, BMR does indeed appear to be elevated compared to terrestrial mammals; however, I argue that this result might be an artifact of confusion over how to apply methodological standards developed for animals in air to animals that spend most to all of their lives under water. I also show that when data are filtered to only include empirical measurements on wild animals, the FMRs of marine mammals are comparable to those of terrestrial mammals, and are in fact indistinguishable from those of terrestrial carnivores. In addition, I describe considerable variability in FMR between the different marine mammal groups. These results indicate that many of the observable similarities between the different groups are superficial and that we cannot make predictions about the metabolic energy demand of one species based on measurements from another without risk of serious errors in estimates of prey requirements. These results also highlight the importance of a careful approach to comparative studies, especially as new data on a broader range of species become increasingly available.

# Chapter 2

# Free-swimming elephant seals have low field metabolic rates that are sensitive to an increased cost of transport

**JL Maresh, SE Simmons, DE Crocker, BI McDonald, TM Williams, DP Costa**

## Abstract

Widely-ranging marine predators often adopt stereotyped, energy-saving behaviors to minimize the energetic cost of transport while maximizing energy gain. Environmental and anthropogenic disturbances can disrupt energy balance by prompting avoidance behaviors that increase transport costs, thereby decreasing foraging efficiency. We examined the ability of 12 free-ranging, juvenile northern elephant seals (*Mirounga angustirostris*) to mitigate the effects of experimentally increased transport costs by modifying their behavior and/or energy use in a compensatory manner. Under normal locomotion, elephant seals had low energy requirements (106.5 ± 28.2 kJ $kg^{-1}$ $d^{-1}$), approaching or even falling below predictions of basal requirements. Seals responded to a small increase in locomotion costs by spending more time resting between dives (149 ± 44 s)

compared to matched control treatments (102 ± 11 s) ($p < 0.01$). Despite incurred costs, most other dive and transit behaviors were conserved across treatments, including fixed, rhythmic swimming gaits. Because of this, and because each flipper stroke had a predictable effect on total costs ($p < 0.001$), total energy expenditure was strongly correlated with time spent at sea under both treatments, ($p < 0.0001$). These results suggest that transiting elephant seals have a limited capacity to modify their locomotory behavior without increasing their transport costs. Based on this, we conclude that elephant seals and other ocean predators occupying similar niches may be particularly sensitive to increased transport costs incurred when avoiding unanticipated disturbances.

## List of symbols used

| | |
|---|---|
| BMR | basal metabolic rate (kJ $kg^{-1}$ $d^{-1}$) |
| COT | cost of transport |
| CPS | cost per stroke (J $kg^{-1}$ $stroke^{-1}$) |
| FMR | field metabolic rate (kJ $kg^{-1}$ $d^{-1}$) |
| Sn | total number of flipper strokes |
| $t$ | time at sea ($d^{-1}$) |
| TEE | total energy expenditure (kJ $kg^{-1}$) |

## 2.1 Introduction

For aquatic animals, the cost of transport (COT, the energetic cost of covering a unit distance) is a substantial component of foraging efficiency; moving through water can be energetically expensive, as drag increases exponentially with increased swimming speed (Fish, 1994; Acevedo-Gutierrez et al., 2002). Swimming behaviors should therefore contribute to an optimization of foraging strategies by reducing COT. Some marine mammals, for example, minimize energy invested in locomotion by swimming at optimal speeds and depths (Williams, 1989; Sato et al., 2007), and utilizing their negative buoyancy to passively glide or drift during descent (Crocker et al., 1997; Skrovan et al., 1999; Costa and Gales, 2000; Williams et al., 2000; Crocker et al., 2001; Watanabe et al., 2006). In Weddell seals, the amount of time spent actively swimming shows a strong relationship with overall costs, such that each propulsive flipper stroke incrementally increases energy expenditure in a predictable manner (Williams et al., 2004a). This is likely the case for other aquatic animals (Wilson et al., 2006; Insley et al., 2007), but empirical measurements of swimming effort in highly migratory pelagic species are difficult to obtain due to the animals' elusive behaviors and far-ranging movements. Data logging instrumentation such as time-depth recorders and video cameras allow documentation of locomotory behaviors, but without an understanding of the associated energetic costs that would be necessary to quantitatively examine swimming effort.

Modification of energy-saving behaviors as a response to local disturbance or food stress can increase swimming effort by increasing the amount of time and energy spent in locomotion, resulting in lowered foraging efficiency and, therefore, lowered fitness (Costa, 2012). Marine mammals may be particularly vulnerable to disturbance as an increased COT would be superimposed on the already elevated energetic demands prescribed by endothermy in water and carnivory (McNab, 1986a; Dejours, 1987; Nagy, 1987; Speakman and Krol, 2010; Hudson et al., 2013). For example, northern elephant seals demonstrate increased foraging trip durations, increased travel time between foraging patches and reduced pup survivorship during severe El Niño years (Crocker et al., 2006). Similar effects on foraging economics can result as an avoidance response to anthropogenic disturbance. For example, avoidance of boat traffic was estimated to reduce energy intake by 18% for resident killer whales compared to individuals in a nearby vessel-exclusion marine protected area (Williams et al., 2006). As disruptive human ocean-based activities intensify, and as prey resources shift in response to climate change, understanding the efforts marine mammals make acquiring resources, and the behaviors that optimize these efforts, becomes increasingly important (Boyd et al., 2008). However, little is understood about the bioenergetics and routine behaviors of these cryptic animals in general let alone how environmental change or anthropogenic disturbance might modify them.

One approach to addressing questions of disturbance to marine mammals is to measure behavioral and physiological responses to artificially increased transport costs (Boyd et al., 1997; Cornick and Horning, 2003). This concept was validated with captive Steller sea lions (*Eumetopias jubatus*), whereby increasing COT by increasing hydrodynamic drag had effects on foraging behavior and efficiency comparable to a decrease in prey availability under standard locomotion (Cornick et al., 2006). Whether due to increased search time when prey encounter rates were low, or increased locomotion costs with added drag, swimming effort increased because sea lions were working harder to find and capture prey (Cornick et al., 2006).

The logistical challenges of working with wild marine mammals have traditionally limited the use of this added-drag approach in studies of free-ranging animals. The northern elephant seal (*Mirounga angustirostris*, Gill 1866), however, is an unusually tractable study species. Elephant seals have a life history schedule that, together with their large body size, facilitates the attachment and retrieval of archival tagging instrumentation, resulting in a rich database of information on the at-sea foraging success and migration behavior of this species. In addition, northern elephant seals, like many marine predators (Polovina et al., 2001; Ayers and Lozier, 2010; Block et al., 2011), exploit resources throughout the northeast Pacific Ocean by tracking large-scale oceanographic features concentrating prey (Simmons et al., 2010; Robinson et al., 2012). Collectively, these factors make the northern elephant seal an ideal study system by which to gain insight into the effects of disturbance on less accessible marine species filling similar ecological niches.

The purpose of this study was to examine the impacts of increased transport costs on the swimming behaviors and bioenergetics of free-ranging northern elephant seals. Specifically we aimed to determine (1) the at-sea costs of locomotion for swimming seals; (2) which aspects of behavior are measurably affected by increased locomotion costs and how seals might mitigate those costs; and (3) whether there are predictable relationships between these costs and the suite of diving and swimming behaviors most commonly measured in long-term tracking programs. To achieve these objectives, drag-inducing devices were deployed on seals to simulate disturbance and reduce performance, and potential behavioral changes were monitored using time-depth recorders (TDRs), GPS tracking devices, and tri-axis accelerometers. Metabolic costs were measured simultaneously using the doubly-labeled water method (Nagy, 1983; Speakman, 1997), and a cost-per-stroke approach (Williams et al., 2004a) was used to model the relationship between individual strokes and total locomotion costs under both conditions (normal swimming, and with added drag). Using each seal as its own control, we used a short-term double translocation protocol (Andrews et al., 1997; Oliver et al., 1998; Webb et al., 1998b; Costa et al., 2003) in which elephant seals were relocated from their haul-out site along the northern side of the Monterey Bay in central California to the southern side of the Bay (Fig. 2.1). Seals captured and translocated just after returning from a long foraging trip will usually return to their rookery within one week. While crossing deep water, homing elephant seals demonstrate diving patterns similar to naturally migrating seals, providing valid insights into the swimming behaviors of free-ranging seals. To our knowledge, this study is the first to simultaneously measure, *in situ*, the behavioral and energetic responses of a wild marine mammal to at-sea disturbance.

## 2.2 Methods

### 2.2.1 Experimental design and animal handling

We experimentally manipulated the COT for twelve 1 – 2.5 year-old northern elephant seals (mass range = 135 – 230 kg) in March – May of 2009 and 2010. Seals were chosen at random in an effort to randomize the sex of the study subjects, however all seals but two (#2 and #4) were female. We chemically immobilized the seals for instrument attachment and recovery using established protocols (Le Boeuf et al., 1988; Le Boeuf et al., 2000). Each seal was weighed upon initial capture by suspension in a canvas sling from a tripod using a Dyna-Link scale (1,000 ± 1 kg). In most cases, seals were reweighed in subsequent handlings; for the remaining (N = 7 of 32 handlings), mass was estimated based on the average daily percent mass loss of weighed seals of 0.37% (ordinary least squares (OLS) linear regression, $r^2 = 0.24$, $F_{1,12} = 4.465$, $p = 0.06$), which did not differ between treatments (ANCOVA, $F_{1,8} = 0.294$, $p = 0.60$).

Using each seal as its own control, we performed double translocation experiments, transporting seals twice by truck from their haul-out rookery at the Año Nuevo State Reserve in California, USA (37° 6' N, 122° 18' W) and releasing them into the southern end of the Monterey Bay, near the Hopkins Marine Station (36° 37' N, 121° 54' W) (approximately 50 km straight distance across the bay; Fig. 2.1). Each seal was fitted with a wooden block ("drag block") representing an approximately 7% increase in cross-sectional area in order to elevate the cost of transport during one return trip. The blocks consisted of a 12 x 10 x 9 cm wooden cube wrapped with splicing tape, and filled with lead weights to ensure neutral buoyancy in water. The drag block was placed along the back in line with other instrumentation, at the position of the animal's maximum girth. The order of the treatments – control (no drag block) or drag treatment (added drag block) – was alternated between subjects to control for an order effect. Behavioral and energetics data were recorded simultaneously during both return trips to Año Nuevo; these measurements are described in detail below.

### 2.2.2 Data collection and processing: behavior

For each seal we recorded coarse-scale dive and transit behaviors during homing under both treatments using TDR and GPS tracking instrumentation (Wildlife Computers, Belleview, WA, USA: Mk9 archival tag, 1-s sampling rate and Mk10-AFB transmitting fast-GPS tag, ~45-s repetition rate, respectively). Raw GPS tracks were truncated according to departure/arrival times identified using the diving record, and then processed using a speed/turn-angle filter to remove unlikely position estimates. The raw time-series of depth measurements were processed in MatLab using the IKNOS toolbox (Y. Tremblay, unpublished program). To make behavioral observations between treatments comparable, only data recorded during directed transit across the bay were used in analysis of diving and transiting behaviors (Fig. 2.1).

For the six seals measured in 2010, flipper strokes were additionally monitored using 3-axis accelerometer/magnetometers (Wildlife Computers MK10-style prototype, 16-Hz sampling rate). The raw time-series of accelerometry measurements were truncated according to departure/arrival times identified using the diving record, and flipper strokes isolated using a custom-written program in Igor Pro 6.22A (WaveMetrics, Inc., USA). In brief, side-to-side flipper movements were detected as fluctuations in the transverse axis – "swaying" acceleration – and the static (positional) component was separated from the dynamic (movement) component using a 1-Hz low-pass filter (Sato et al., 2003; Mitani et al., 2010). The remaining peaks and troughs in the dynamic swaying acceleration with amplitudes greater than a threshold value were considered to be individual flipper strokes and were used in analyses. Amplitude thresholds differed between seals due to small differences in accelerometer placement during attachment, and perhaps due to inherent differences between seals, but thresholds values were held constant between treatments within individuals.

Only data recorded during directed transit across the bay were used in analysis of flipper stroking behaviors (Fig. 2.1).

### 2.2.3 Data collection and processing: energetics

At-sea metabolic rates of homing seals were measured using the doubly-labeled water method (Nagy, 1980, 1983; Speakman, 1997), which has been validated for use with seals (Costa, 1987; Sparling et al., 2008). Prior to its first release, each seal was given a 5-mL intravenous injection of sterile HTO containing 1.0 mCi/mL (2009) or 0.2 mCi/mL (2010) of the heavy hydrogen isotope (H-3), and 71-mL (2009) or 25-mL (2010) of sterile $H_2O^{18}$ containing 24% and 68% enrichment of the heavy oxygen isotope (O-18), respectively. These amounts were determined based on the average mass of juvenile (1 – 2.5 yrs) elephant seals (180 kg), a desired initial enrichment of approximately 1 g oxygen isotope per 1 kg of animal, the half-life of O-18 (4.97 days), and the rate of water turnover in elephant seals (very slow) relative to the maximum anticipated return date of translocated seals (less than 2 weeks). Seals were not translocated a second time if blood samples were collected more than 11 days after the initial translocation, as blood O-18 levels would have been approaching natural background levels. For this reason, four of the 12 seals involved in this study were considered unsuitable for a second translocation: two returned to Año Nuevo after 11 days, and two hauled out at alternative locations that delayed accessibility to the seals for timely collection of blood samples.

Isotopes were allowed 90 minutes post-injection to equilibrate with the seals' body water pools (Kelso et al., 2012), and blood samples were taken pre-injection, post-equilibration, and as soon as possible upon each seal's two return arrivals at Año Nuevo. Blood samples were kept on ice in a cooler while in the field. Within 6 hours of collection, samples were centrifuged for 10 minutes at 3000 rpm, and the serum was decanted into 5-ml screw-cap vials and placed in -20°C storage until analysis. Specific activity of tritiated water was determined in triplicate by scintillation spectrometry (Beckman LS 6500, Beckman Coulter, Fullerton, CA) of water obtained from serum using the dry ice distillation method (Ortiz et al., 1978). Specific activity of oxygen-18 water was determined by mass ratio spectrometry of water distilled from blood serum (Metabolic Solutions, Nashua, NH).

Initial total body water (TBW) was determined using the initial dilution space of oxygen-18, while final TBW was calculated as the percentage initial body water multiplied by the seal's final mass (Nagy, 1980, 1983; Speakman, 1997). $CO_2$ production was calculated using Speakman's (1997) two-pool equation due to the seals' large body size and in order to account for isotope fractionation (Sparling et al., 2008).

To determine whether seals were foraging while homing, we assigned behaviors to each dive using a custom-written dive classification program in Matlab (P. Robinson, unpublished program). Classification was based on dive shape as described in, for example, Le Boeuf et al. (1992) and Crocker et al. (1997). With only one exception (see Results), dive typing was not suggestive of the complex activities putatively indicative of foraging, but rather of simple transiting and resting behaviors only (Le Boeuf et al., 1992; Crocker et al., 1997; Robinson et al., 2007; Robinson et al., 2010). As such, we assumed homing seals were fasting and exclusively metabolizing fat, and thus used an energy conversion factor of 26.81 kJ $L^{-1}$ $CO_2$ in calculating field metabolic rates (Costa, 1987). As these measurements included variable amounts of onshore FMRs for each seal (range = 8 – 78%, mean = 37 ± 21%), FMRs were corrected for any time spent on land during the measurement period in order to estimate at-sea FMRs. FMR was normalized to estimate the at-sea component by plotting total FMR as a function of time at sea and then using least-squares linear regression equations to predict the FMR for each seal for its respective percentage of time at sea (Costa and Gales, 2003).

We determined the CPS for the six seals in this study for which we were able to measure both energetics and flipper stroking dynamics concurrently by dividing total at-sea field costs by the total number of flipper strokes measured. In addition, we calculated the cost of locomotion under both treatments as the difference between the total at-sea FMR of each seal and its basal maintenance costs according to the equation:

$$\text{Locomotion cost} = \text{FMR}_{\text{at-sea}} - (\text{BMR}*t) \qquad (2.1)$$

where locomotion cost and $\text{FMR}_{\text{at-sea}}$ are in kJ $kg^{-1}$, BMR is in kJ $kg^{-1}$ $d^{-1}$, and $t$ is the duration of the measurement period in days (modified from Williams et al. (2004a) eq. 1). We assumed the BMR of swimming seals to approach Kleiber (1975) predictions as has been demonstrated in previous experiments on quiescent, submerged pinnipeds (Webb et al., 1998a; Costa, D. P. and Williams, T. M., 1999; Hurley and Costa, 2001; Williams et al., 2004a; Costa, 2009). We examine the evidence for, and the implications of, this assumption in the discussion.

### 2.2.4 Data analysis

Dive duration, inter-dive rest duration, dive depth, descent and ascent rates, relative bottom time, and swimming effort during directed transit across the Monterey Bay were compared between treatments (hereafter referred to collectively as “dive variables”). For each dive, duration was measured as the total amount of time required for one complete dive cycle (descent, bottom time and ascent); rest duration was expressed as the duration of the surface interval between dives (i.e., time spent resting between dives); depth was expressed as the maximum depth achieved; and bottom time was expressed relative to dive duration. To calculate bottom time, the bottom phase was determined by changes in the descent and ascent slopes of the seal relative to maximum depth. In brief, the start of the bottom phase was designated by the first point within 70% of the seal’s maximum depth where vertical speed fell below 20% of maximum speed during descent. The end of the bottom phase was determined in reverse. Finally, swimming effort was determined by measurements of flipper stroking frequency and amplitude, as described above. As stroking amplitude depends on the placement of the instrumentation on the animal, which varied slightly across individuals, amplitudes between treatments were only compared within individuals, and thus are reported here as relative values only.

Due to the non-linear, nested structure of the data, generalized additive mixed effects models (GAMMs) were used to model the effects on the dive variables of the continuous explanatory variables: time of day (hr), elapsed time into trip, and mass, and the factor explanatory variables: treatment (control or added drag), deployment number (whether it was the animal's first or second trip), and individual animal (random effect). Separate models were fitted for each of the response dive variables listed above. The intercept of these models was permitted to vary randomly across animals and any within-seal autocorrelation was modeled using a first-order autoregressive autocorrelation structure to account for repeated measurements on the same animal during a trip. A power variance function structure was used to model within-group heteroscedastic error, allowing the variance to increase as a power of the absolute fitted values. Candidate models were of the form:

$$Y_{ij} = \beta_0 + a_i + f_1(\text{hr}) + f_2(\text{Elapsed Time}) + \beta_1\text{Treatment} + \beta_2\text{Mass} + \beta_3\text{Deploy} + \varepsilon_{ij}$$

where $Y_{ij}$ is the *j*th observation from the *i*th animal; $\beta_0$ is the overall intercept; $a_i \sim N(0, \sigma^2_a)$ is the random effect (intercept) of the *i*th animal; $f_1$ and $f_2$ represent penalized, cyclic cubic regression spline functions with $f_1$ having the same start and end point; $\beta_1$, $\beta_2$, and $\beta_3$ are coefficients; and $\varepsilon_{ij}$ is the residual random error term with specified power variance function and correlation structure. Interactions between the smooth and factor terms were also modeled, where appropriate.

Analyses were performed using the ‘gamm’ function (with restricted maximum likelihood method) of the ‘mgcv’ package (Wood, 2006) in R 2.15.1 (R Development Core Team, 2013). All model combinations were fitted with best model fits based on the lowest Akaike information criteria corrected for small sample size (AICc), and AICc differences less than 2.0 were considered substantial evidence for competing models, with preference given to models with fewer terms (Burnham and Anderson, 2002; Zuur, 2009). Residual plots and partial residual plots were examined to assess model fits. The significance of terms included in the final models was examined using approximate *p*-values from the ‘mgcv’ output.

We used OLS models to explore potential predictive relationships between number of flipper strokes, FMR, time spent at sea, cost per stroke and mass. We used data from the entire trip in these comparisons, as the resolution of the metabolic data did not make it possible to parse out FMR during directed transit across the bay from the total FMR of the entire trip. In each pairwise comparison, we tested for a treatment effect by including the interaction between the response variable and treatment (control or added drag) in the model. Pooled data were used where no significant treatment effect was detected, but kept separate otherwise. In the latter case, regression equations are not presented for data under the drag treatment as, representing an artificial situation, they would have no biologically relevant predictive value.

## 2.3 Results

Table 2.1 summarizes the variation in numbers and types of samples collected from the 12 seals involved in this study. In contrast to all other translocations, seal #6 was in positive energy balance after her second trip, which was indicative of foraging. In addition, 24% of her dives during this time were classified as foraging dives, compared to 0-6% (mean = 1.5 ± 0.02%) in all other translocations (Fig. 2.2). For these reasons, data for seal #6's second trip were excluded from energetics analyses.

### 2.3.1 Effects of increased transport costs on metabolism, diving behavior and swimming mechanics

Field metabolic rates (FMRs) of free-ranging, control seals averaged 106.5 (±28.2) kJ $kg^{-1}$ $d^{-1}$, with younger seals generally having higher metabolisms than older seals (Table 2.2). Seals were working approximately 1.6 times harder with the added drag than without (Welch two-sample t-test, $t = -4.8165$, $df = 16.619$, $p < 0.001$), with FMRs averaging 175.2 kJ $kg^{-1}$ $d^{-1}$. This increased effort was reflected in some of the dive behaviors (Table 2.3).

Results from the GAMMs indicate that seals under the drag treatment increased time spent at the surface resting between dives by 46% ($p < 0.01$). In addition, seals under the drag treatment ascended from their dives approximately 13% slower ($p < 0.05$), and the magnitude of this effect decreased with increasing body size (i.e., the ascent rate of larger seals was less affected by added drag than that of smaller seals) ($p < 0.005$). Likewise, seals under the drag treatment descended to depth approximately 10% slower ($p < 0.05$), although with no interaction effect of mass.

To determine the cause of changes in ascent and descent rates, we compared swim speed and pitch angle between treatments for the three seals with matched treatments and carrying accelerometers (paired Students t-test) (Table 2.4). For each dive, pitch was calculated using information from the acceleration sensor along the longitudinal axis of the seal, after correcting for the placement of the instrument on the seal (Sato et al., 2003). In combination with vertical speed from the TDR, pitch angle was used to calculate true swim speed (Sato et al., 2003) in one-second intervals. Data were suggestive of slower swim speeds ($p = 0.07$) and shallower diving angles during descent ($p = 0.13$) under the drag treatment, with no clear effect of added drag on swim speed or diving angles during ascent ($p = 0.30$ and 0.51, respectively). Individual responses varied, which, collectively with our small sample size, precludes firm conclusions in regards to changes in swim speed or pitch angle under the drag treatment. However, regardless of the specific mechanism, slower ascent and descent rates were likely an artifact of the hydrodynamic effects of the drag block on forward propulsion, rather than an actual behavioral response.

For the remaining dive variables tested, seals conserved many of their swimming behaviors across both treatments despite the elevated energetic costs of added drag. There were no differences in dive depth or duration, or time spent at depth (bottom time) relative to the entire dive duration (Table 2.3). Surprisingly, the elevated energetic effort associated with the drag treatment did not measurably alter swim gait: neither flipper stroking frequency (1459 ± 117 $h^{-1}$) nor amplitude differed across treatments. This result was consistent when stroking mechanics of different portions of the dive cycle (surface, descent, bottom and ascent) were compared across treatments, as well as when averages of entire dive cycles were compared.

### 2.3.2 Predicting costs during standard locomotion

As expected, total number of flipper strokes (Sn) increased linearly with total time spent at sea (Fig. 2.3) according to the equation:

$$\mathrm{Sn} = 38629 * t - 10331 \qquad (2.2)$$

where $t$ is time in days ($r^2 = 0.97$, $F_{1,7} = 330.3$, $p < 0.0001$). There was no effect of treatment on this relationship ($p = 0.25$), so eq. 2.2 includes data pooled from seals under both treatments. Using eq. 2.2, we were able to approximate the total number of flipper strokes for the six seals in this study for which time-at-sea was measured but stroking information was not (Table 2.5), and compared the number of calculated strokes with the total energy expenditure measured for each. As expected, total at-sea energy expenditure increased linearly with the number of flipper strokes (Fig. 2.4) according to the equation:

$$\text{TEE} = 0.0039^{*}\text{Sn} - 87.62 \tag{2.3a}$$

where TEE is total energy expenditure in kJ kg$^{-1}$, and Sn is the total number of flipper strokes ($r^2 = 0.98$, $F_{1,6} = 342.1$, $p < 0.001$). There was a significant effect of treatment on this relationship ($p < 0.01$), so eq. 2.3a includes data from seals under the control treatment only. Eq. 2.3a also includes the six seals for which flipper stroke number was calculated using eq. 2.2. When those six seals are excluded and only measured seals used, the relationship between total at-sea energy expenditure and the number of flipper strokes is similar (ANCOVA, $F_{1,8} = 3.901$, $p = 0.09$):

$$\text{TEE} = 0.0041^{*}\text{Sn} - 139.10 \tag{2.3b}$$

($r^2 = 0.99$, $F_{1,2} = 533.5$, $p < 0.005$). Again, there was a significant effect of treatment on this relationship ($p < 0.05$), so eq. 2.3b includes data from seals under the control treatment only. These results suggest that the magnitude of the effect of each flipper stroke on total energy costs (cost per stroke, or CPS) is approximately 4 J kg$^{-1}$ stroke$^{-1}$ in free-ranging control seals, although this is somewhat higher than measured (mean = 3.0 ± 0.77 J $kg^{-1}$ $stroke^{-1}$, N = 8). In comparison, CPS increased by approximately 71% for the seals under the drag treatment (mean = 5.1 ± 0.78 J $kg^{-1}$ $stroke^{-1}$, N = 11). As was the case with the control seals (eqs. 2.3a and 2.3b), the relationship between total at-sea energy expenditure and number of flipper strokes was similar under the drag treatment regardless of which seals were included in the regression (ANCOVA for slopes, $F_{1,13} = 0.53$, $p = 0.96$; ANCOVA for intercepts, $F_{1,14} = 0.57$, $p = 0.46$).

Under both treatments, CPS tended to decrease with body size (Fig. 2.5A), although this effect was not significant ($p = 0.08$ and 0.36 for seals under the control and drag treatments, respectively). While not statistically different (ANCOVA, $F_{1,9} = 0.3$, $p = 0.60$), the intercepts in eqs. 2.3a and 2.3b, together with the low p-value comparing the two intercepts ($p = 0.09$) also support the idea of a lower CPS for larger individuals: seals whose flipper strokes were directly counted were, on average, larger and older than seals whose flipper strokes were only estimated using eq. 2.3a (Tables 2.1 and 2.2), again indicating a possible size effect on CPS. This trend was likely associated with the age of the animal rather than mass per se: the CPS for yearling control seals averaged 3.45 J $kg^{-1}$ $stroke^{-1}$ compared to 2.58 J $kg^{-1}$ $stroke^{-1}$ for 2 – 2.5 year olds (OLS linear regression, $r^2 = 0.69$, $F_{1,6} = 16.67$, $p < 0.01$), suggesting increased costs in younger animals that may not be detectable with our small sample size.

This cost, however, is a whole-body cost and therefore incorporates the basal metabolic rates (BMRs) of the seals (and therefore, gliding). After accounting for the contribution of predicted BMR (Kleiber, 1975) to FMR using eq. 2.1, locomotion costs represented approximately one-quarter of the control seals' at-sea energy expenditure. There was no effect of body size on the CPS associated strictly with locomotion under the control treatment ($p$ = 0.35), but there was a decreasing tendency under the drag treatment (Fig. 2.5B), although this effect was not statistically significant ($p$ = 0.13). This suggests that locomotion costs during normal swimming are the same for each seal, regardless of body size (or age), and so the increased total CPS of younger seals is driven by elevated juvenile metabolism instead.

Total at-sea energy expenditure increased linearly with time spent at sea (Fig. 2.6) according to the equation:

$$\mathrm{TEE} = 163.0{*}t - 142.4 \tag{2.4}$$

where TEE is in kJ kg$^{-1}$, and $t$ is time in days ($r^2 = 0.98$, $F_{1,6} = 274.1$, $p < 0.0001$). There was a significant effect of treatment on this relationship ($p < 0.05$), so eq. 2.4 includes data from seals under the control treatment only.

Finally, to explore the potential to use other, more commonly measured behaviors to predict the at-sea energy expenditure of wild northern elephant seals not instrumented with accelerometers, we compared the number of strokes calculated using time at sea (eq. 2.2) with those calculated using a constant flipper stroking frequency of 1459 strokes h$^{-1}$ (Table 2.5). The number of strokes calculated using time at sea and a constant stroke frequency were within 11 ± 5% and 9 ± 5% (absolute mean errors) of true values, respectively, demonstrating their effectiveness in estimating at-sea energy expenditure (eq. 2.3a) when stroking information is not directly available.

## 2.4 Discussion

The analyses presented here demonstrate the energetic requirements of free-ranging elephant seals, their behavioral responses to increased locomotion costs, and the predictive relationships between these costs and time spent swimming at sea – a simple metric commonly measured in long-term tracking programs. Data from this experiment specifically show that (*i*) free-swimming elephant seals have low field metabolic costs that approach predictions of mammalian basal metabolism with increasing age; (*ii*) the effect of each individual flipper stroke on fuel reserves decreases as seals mature; (*iii*) the amount of time spent at sea has a predictable effect on the total number of flipper strokes, overall field metabolic rate, and total energy expenditure of northern elephant seals; and (*iv*) artificially increased transport costs are associated with longer resting periods between dives and slower dive descent and ascent rates, but are not associated with changes in dive duration, maximum dive depth, time spent at depth, or swimming mechanics (flipper stroking frequency and amplitude).

### 2.4.1 Ecological Implications: Field metabolic rates and locomotion

An animal's FMR includes costs associated with both locomotion and basal maintenance. Thermoregulation can impose additional costs, however these costs are expected to be trivial for elephant seals adapted to the range of water temperatures encountered in Monterey Bay (Noren, 2002). Feeding and digestion will also increase costs, however we assume these costs, if present, to be minor in their overall contribution to the total FMRs of the seals in this study. Seal #6 was likely foraging extensively during her second homing trip, but a comparison of her diving behavior to that of the remaining seals indicates simple transiting and resting behaviors only during all other translocations (Le Boeuf et al., 1992; Crocker et al., 1997; Robinson et al., 2007; Robinson et al., 2010) (Fig. 2.2). For these reasons we are confident that our FMR measurements generally included only those associated primarily with locomotion and basal metabolism.

We report the mass-specific FMR of free-ranging seals to be 106.5 ± 28.2 kJ $kg^{-1}$ $d^{-1}$, a rate that is approximately 1.3 times above predicted BMR (Kleiber, 1975) (Table 2.2). Locomotion costs were therefore responsible for approximately one-quarter of the total at-sea energy expenditure of juvenile elephant seals. As expected, when separated by age class, yearling seals had higher FMRs than older seals, averaging 1.5 and 1.0 times predicted BMR, respectively. Seals #7 and #8 showed FMRs lower than predicted BMR. They were the largest seals in this study (211 and 229 kg), suggesting that larger, adult elephant seals are capable of metabolic suppression while diving. FMR values reported here are also in agreement with those measured in captive juvenile elephant seals diving in a metabolic chamber (Webb et al., 1998a) but somewhat lower than the 1.9 times BMR reported by Williams et al. (2004a) for adult Weddell seals diving for 18.35 minutes, the average dive duration of elephant seals in the present study. These results suggest that northern elephant seals, even as juveniles, have low metabolic costs relative to other seals, and indeed, relative to other carnivores which typically operate at 2.0 – 4.7 times predicted BMR on land and 4.9 – 6.4 predicted BMR in water (Reilly and Fedak, 1991; Costa, 1993; Nagy et al., 1999; Nagy, 2005; Costa, 2009; Speakman and Krol, 2010).

Dividing total energy expenditure by the number of flipper strokes recorded gives us a predictable effect of each stroke on fuel stores: approximately 3.0 J $kg^{-1}$ $stroke^{-1}$. We found no statistically significant effect of body size on stroke costs for elephant seals, although the data are suggestive of a decreasing trend with mass (Fig. 2.5) that may not have been detectable given the small sample size. However, Tift et al. (2013) and Houser et al. (2012) measured a 7-10% reduction in resting metabolism between elephant seal pups 2 weeks (mass = 119 ± 18 kg) and 7 weeks post-weaning (mass = 81 ± 20 kg), indicating that the relationship between juvenile and adult metabolism is conditional on the age class of the animal if not actual body size. Indeed, when the two age classes in the current study are separated out, the CPS for yearling seals increases to 3.45 J $kg^{-1}$ $stroke^{-1}$ and decreases to 2.58 J $kg^{-1}$ $stroke^{-1}$ for 2 – 2.5-year-olds. This suggests that, for elephant seals, existence costs decline with age as growth costs decrease and that the true CPS for an adult northern elephant seal is likely at or below 2.58 J $kg^{-1}$ $stroke^{-1}$. This CPS value converges on those measured directly using open-flow respirometry on captive phocids (Innes, 1984; Davis et al., 1985; Fish et al., 1988) and on free-ranging Weddell seals (Williams et al., 2004a) (1.44 – 2.87 J $kg^{-1}$).

### 2.4.2 Basal metabolic rates: marine mammals and juveniles

It is worth examining the assumption of Kleiber (1975) predictions for BMR in the conclusions drawn thus far. There has been much discussion of the validity of measurements of BMR reported for marine mammals (Lavigne et al., 1986; Hurley and Costa, 2001; Williams et al., 2004a; Costa, 2009), with no conclusive results. Traditionally, marine mammals have been reported as having BMRs approximately two times higher than Kleiber predictions for a similarly-sized terrestrial mammal (Lavigne et al., 1986; Williams et al., 2001), approaching values predicted for terrestrial, carnivorous mammals (McNab, 2000). Others have reported values approaching Kleiber predictions (Hurley and Costa, 2001; Williams et al., 2004a). Evidence suggests that much of this discrepancy can be accounted for to some degree by whether the animal is resting at the water surface or is submerged during measurements. For example, Hurley and Costa (2001) reported metabolic rates of 2-3 times expected for sea lions resting on the water surface, but approaching Kleiber predictions during prolonged submergence. Similarly, Weddell seals resting at the water surface are reported as having metabolic rates 1.8 times

(Castellini et al., 1992) and 1.6 times (Williams et al., 2001; Williams et al., 2004a) higher than predicted for terrestrial mammals, but only 1.1 times higher when submerged and inactive (Williams et al., 2004a). Additionally, juvenile elephant seals resting at the water surface are reported as having metabolic rates 1.3 times higher than predicted BMR, but similar to predicted BMR while diving in a metabolic chamber (Webb et al., 1998a). As our study animals spent approximately 90% of their time at sea submerged, we chose to assume Kleiber predictions when factoring BMR into our measurements of overall at-sea energy expenditure in northern elephant seals.

However, the seals in this study were juveniles, and it is typically the case that immature, growing animals have elevated mass-specific BMRs relative to adults. It is thus possible that the BMRs of the seals in this study were underestimated, which would result in an overestimation of locomotion, and therefore stroking, costs. Lavigne et al. (1986) present evidence to suggest that the BMR of immature seals is actually 1.6 times that of Kleiber predictions for adult seals; however, it is not clear that the BMR values used in the Lavigne et al. review (1986) were for individuals at rest, and thus we believe their estimates of BMR in juvenile seals to be overestimates. Indeed, recent studies report resting metabolic rates of newly weaned elephant seal pups of 0.9 – 1.4 Kleiber when submerged and 1.1 – 1.6 Kleiber in air (Noren, 2002; Houser et al., 2012; Tift et al., 2013), supporting the idea that basal costs of even the youngest elephant seals approach Kleiber predictions for adults during submergence.

### 2.4.3 Altered behavior at sea

In this experiment, seals with added drag saw a 65% increase in FMR compared to seals under the control treatment (Table 2.2). The elevated cost under the drag treatment was reflected in only two major alterations to behavior: time spent resting between dives, and descent and ascent rates while diving. Seals with added drag had longer, more variable inter-dive surface intervals (149 ± 44 s) than control seals (102 ± 11 s). This response is consistent with that of Antarctic fur seals who demonstrated longer surface durations when their locomotion costs were artificially increased (Boyd et al., 1997). These results are not unexpected as seals diving with added drag would deplete more of their oxygen reserves during breath-hold, requiring longer recovery times at the surface. In contrast, surface intervals of the control seals in this experiment resembled those of adult elephant seals during natural migrations: short, consistent, and uncorrelated with dive duration or any other measured dive variable (Le Boeuf et al., 1988; Le Boeuf et al., 1992). For all free-ranging northern elephant seals, extended time spent resting at the surface is rare as it leaves the animal vulnerable to surface predators such as white sharks (*Carcharodon carcharias*) and killer whales (*Orcinus orca*) (Le Boeuf et al., 1998), making the response by the seals in this study noteworthy.

Seals with added drag also exhibited 10% slower descent and 13% slower ascent rates during diving (Table 2.3), perhaps due to shallower pitch angles and/or a reduction in swim speeds (Table 2.4). The reduced swim speeds measured here are indicative of a 16-27% increase in drag, if optimal speeds are proportional to $(BMR/drag)^{1/3}$ (Alexander, 1999; Motani, 2002; Sato et al., 2010). Our results are consistent with previous studies showing similar effects of instrumentation on these particular aspects of diving performance in various species (Littnan et al., 2004; Heaslip and Hooker, 2008; Latty et al., 2010). For the seals in the current study, the mechanisms behind slower descent and ascent rates, while unclear, were likely a physical artifact of the hydrodynamic drag added by the block, rather than a behavioral response per se.

None of the remaining dive variables tested here – dive duration, maximum depth, bottom time, stroke frequency or stroke amplitude – were affected by the increased costs associated with the drag treatment. Most surprising was the lack of an effect on stroking mechanics: regardless of effort, stroking amplitude (relative measure) and stroking frequency (1459 strokes $h^{-1}$) remained constant. This was surprising as we expected that, in response to increased drag, amplitude and/or frequency would either decrease in order to reduce costs or increase in order to maintain preferred swim speeds (Wilson et al., 1986; Boyd et al., 1997; Cornick et al., 2006). The stroking mechanics of northern elephant seals appear to be relatively fixed, that is, composed of stereotypic movements coordinated by rhythmic pattern generators similar to the locomotor gaits of tetrapods and others (Grillner and Wallen, 1982, 1985; Duysens and Van de Crommert, 1998; Ijspeert, 2008). Fixed gaits allow for economy of energy expenditure

(Schmidt-Nielsen, 1972; Hoyt and Taylor, 1981; Perry et al., 1988) and are "hard-wired" components of animal locomotion subject to modulation via energetic input: once energy expenditure increases beyond some threshold value, animals will alter stride frequencies and mechanics (i.e., switch gaits) in order to maximize efficiency (Kar et al., 2003). Our results suggest that, despite the increased effort required for forward movement, alternative gaits were not attractive options for seals with added drag – seals either did not reach the inefficiency threshold necessary to trigger a gait switch, or alternative gaits did not improve energy economy. Either way, the stroking frequencies and amplitudes measured here were likely efficient under normal swimming conditions but less so with the added drag, giving rise to the increased FMR under the drag treatment.

### 2.4.4 Predicting the energy requirements of free-ranging animals

Marine mammals occupy high trophic positions and can have disproportionate, landscape-level effects on the structure and function of ecosystems (Bowen, 1997; Estes et al., 1998; Williams et al., 2004b; Estes et al., 2011). However, the hidden behaviors and far-ranging movements of marine mammals make determination of prey-energy requirements particularly challenging for this group. Studies of marine mammal foraging energetics are thus often limited to inferences about the ecology and physiology of free-ranging animals by extrapolation of measurements taken on individuals in captivity (Cornick et al., 2006; Williams et al., 2007;

Liwanag, 2010). For most species, even captive studies are impossible and thus a variety of indirect approaches have been applied in trying to quantify at-sea energetics. These include the use of physiological variables such as heart rate (Williams et al., 1992; Boyd et al., 1995; Butler and Jones, 1997), and behavioral metrics such as swim speed (Kshatriya and Blake, 1988; Hind and Gurney, 1997) as proxies of metabolism, with inherent inaccuracies due to unvalidated or weak relationships and substantial variation between individuals (McPhee et al., 2003).

Our study adds to a very small body of work directly measuring energetic demands on free-ranging marine mammals, including Antarctic fur seals (Arnould et al., 1996) and Weddell seals (Castellini et al., 1992; Ponganis et al., 1993; Williams et al., 2004a); to our knowledge, it is the only to do so for a species outside an Antarctic ecosystem. For the seals in our study, energy expenditure was predictably affected by flipper strokes (Fig. 2.4), the total number of which was directly and strongly correlated with time spent swimming at sea (Fig. 2.3). Because of these relationships, time-at-sea alone could be used as a predictor of total energy expenditure within approximately 10% of true values (Table 2.5), making it possible to estimate the energy requirements of free-ranging, cryptic seals in the absence of direct stroking information (Fig. 2.6).

### 2.4.5 Conclusions

In summary, northern elephant seals demonstrate low existence costs with field metabolic rates approaching and falling below estimates of basal metabolic requirements. This is particularly noteworthy given that the animals in this study were (1) marine mammals, (2) carnivores, and (3) juveniles. Energy expenditure was strongly correlated with time spent at sea as swim gait was fixed and rhythmic, regardless of locomotion costs. Seals working harder during locomotion did not alter gait, resulting in elevated costs, with consequent alterations in diving behavior that did not mitigate these costs. These results indicate that elephant seals may be inflexible in their swimming behaviors, which are best suited for efficient locomotion given the mechanical constraints of movement in water. As current patterns of prey availability and distribution in the North Pacific Ocean shift in response to rapid climate change, elephant seals, like many marine predators, will need to travel farther to track prey fields with high energetic payoff, with predictable effects on energy expenditure and, ultimately, energy balance and foraging success.

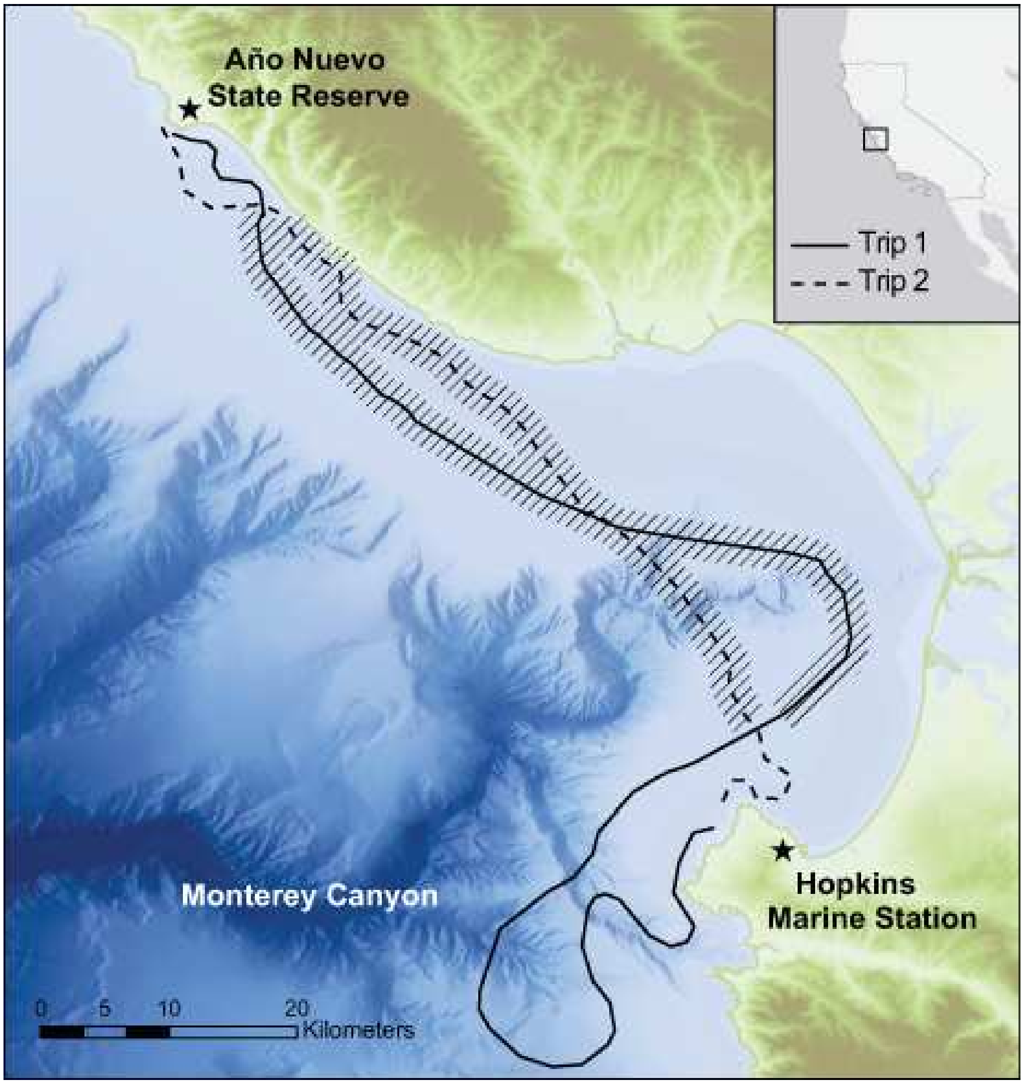

**Figure 2.1. Haul-out (Año Nuevo) and release (Hopkins) sites of translocated seals are approximately 50 km apart across the Monterey Bay.** Surface tracks of one homing seal during both trips are shown as an example. For this seal, Trip 1 was under the control treatment, while Trip 2 was under the added drag treatment. Only portions of the tracks representing transit across the bay (hatched) were used in comparisons of diving behavior and transit rates.

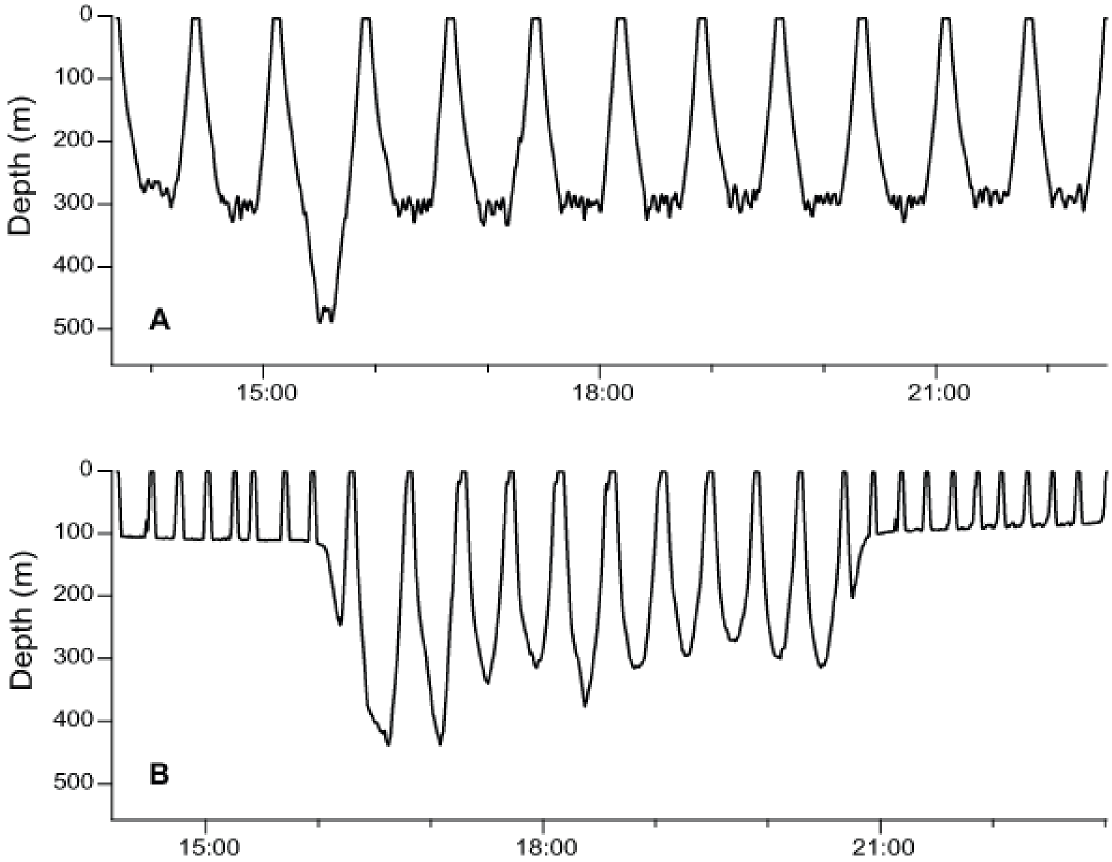

**Figure 2.2. A comparison of dive types shows putative (A) foraging and (B) transit behaviors during similar timeframes for two different translocations.** The top figure was taken from the dive record of seal #6 during her second trip, which included a large proportion of foraging dives (24%) compared to all other translocations (mean = 1.5 ± 0.02%). The bottom figure shows a more typical translocation dive record, with relatively deep u- and v-shaped transiting dives over the canyon flanked by shallow, benthic dives where the seal is following the bottom topography of the Monterey Bay.

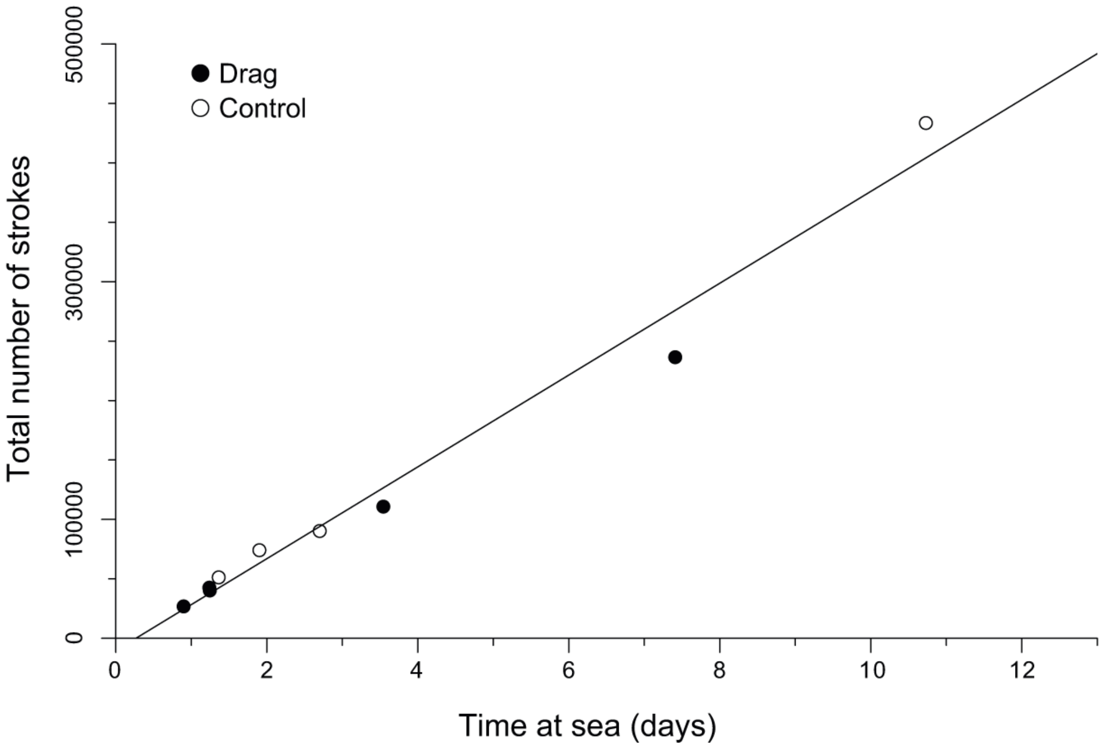

**Figure 2.3. Total number of flipper strokes increased linearly with total time spent at sea (entire measurement period).** This relationship was similar for seals regardless of treatment and can be described by the equation $y = 38629x - 10331$ ($r^2 = 0.97$, $F_{1,7} = 330.3$, $p < 0.0001$).

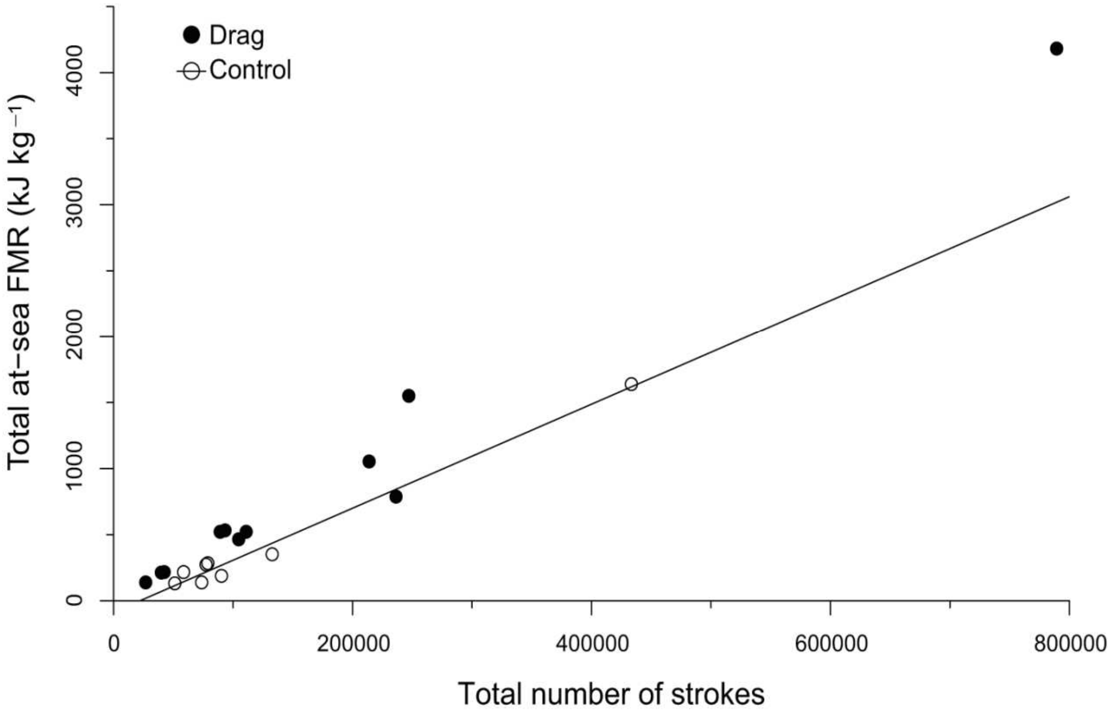

**Figure 2.4. Total at-sea mass-specific energy expenditure increased linearly with total number of flipper strokes for seals swimming normally and for seals swimming with added drag.** This relationship differed between treatments so the regression line is for control seals only and can be described by the equation y = 0.0039x – 87.62 ($r^2$ = 0.98, $F_{1,6}$ = 342.1, $p <$ 0.001).

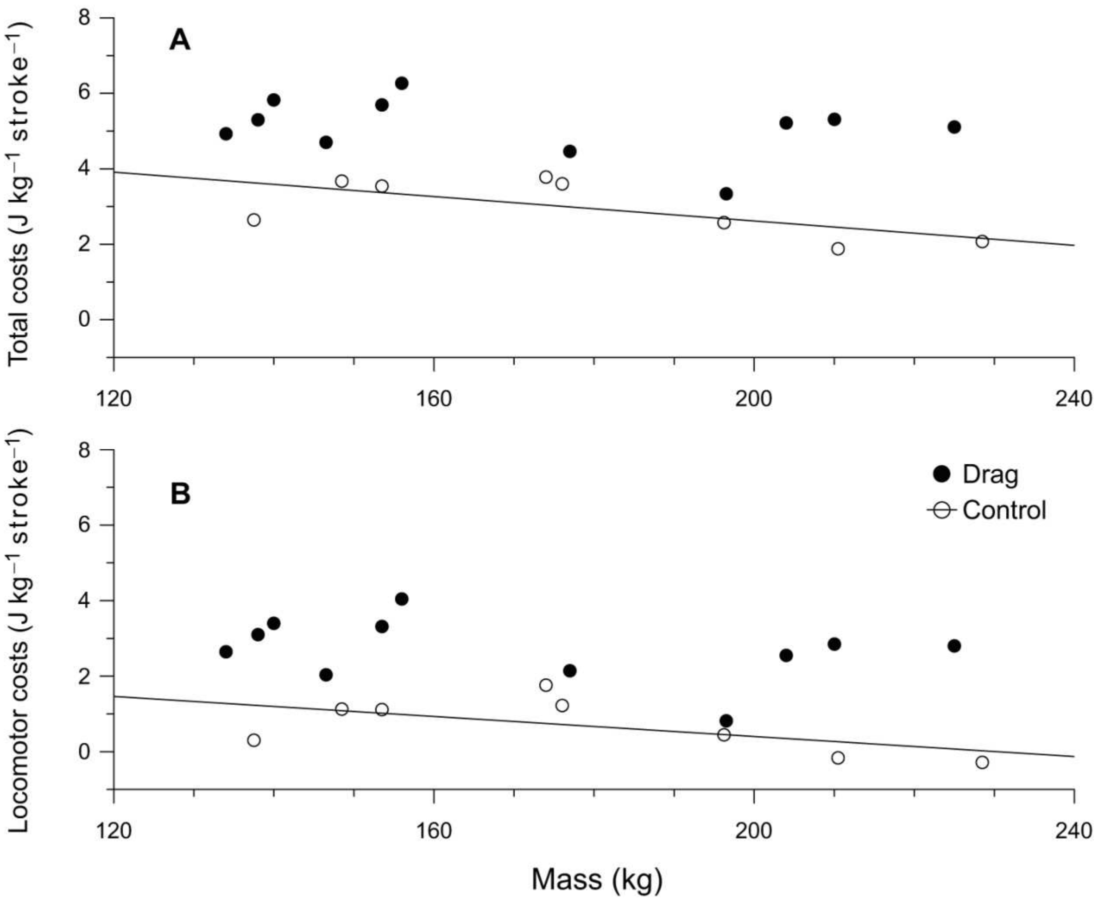

**Figure 2.5. Total (A) and net (B) stroking costs had a tendency to decrease linearly with mass, although these relationships were not statistically significant.** This relationship differed between treatments so the regression lines are shown for control seals only.

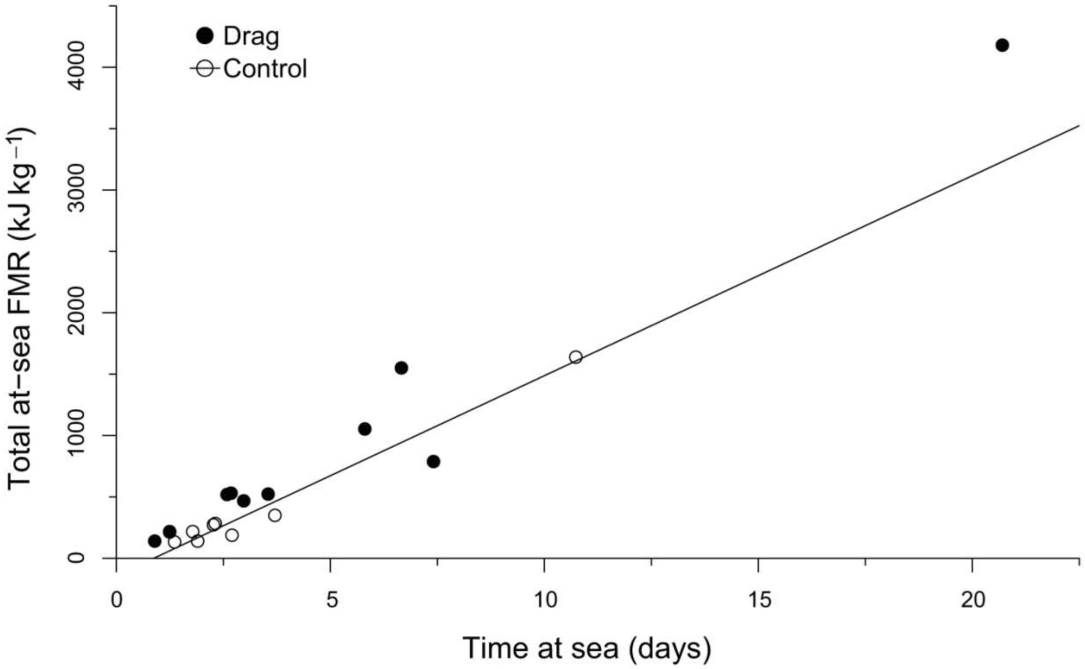

**Figure 2.6 Total at-sea mass-specific energy expenditure increased linearly with time spent at sea.** This relationship was similar for seals regardless of treatment and can be described by the equation y = 163.0x – 142.4 ($r^2 = 0.98$, $F_{1,6} = 2741$, $p < 0.0001$).

**Table 2.1. Summary of variation in numbers and types of samples collected from the 12 seals in this study.** Blank cells indicate no data collection. Under Treatment type, "Control" indicates seals swimming normally and "Drag" indicates seals swimming with added drag.

| Seal | Treatment | | Behavior | | | At-sea field metabolic rate |
|---|---|---|---|---|---|---|
| | Control | Drag | Diving | Tracking | Stroking | |
| 1 | x | x | x | x | | x |
| 2 | x | x | x | x | | x |
| 3 | x | x | x | x | | x |
| 4 | | x | x | x | | x |
| 5 | x | x | x | x | | x |
| 6 | x | x | x | x | | x |
| 7 | x | x | x | x | x | x |
| 8 | x | x | x | x | x | x |
| 9 | | x | x | x | x | x |
| 10 | x | x | x | x | x | x |
| 11 | | x | x | x | x | x |
| 12 | x | | x | x | x | x |

**Table 2.2. At-sea field metabolic rates of the 12 seals in this study.** Mass was measured just prior to release. "Treatment" refers to seals swimming with (D = drag) (grey shading) and without (C = control) added drag. "Kleiber" is a multiplier of Kleiber (1975) predictions of mammalian basal metabolic rate.

| Seal | Age (YO) | Mass (kg) | Treatment | At-Sea FMR (kJ kg$^{-1}$day$^{-1}$) | Kleiber |
|---|---|---|---|---|---|
| 1 | 1-1.5 | 149 | C | 120.8 | 1.4 |
| | | 140 | D | 201.6 | 2.4 |
| 2 | 1-1.5 | 177 | D | 156.7 | 1.9 |
| | | 176 | C | 123.2 | 1.5 |
| 3 | 1-1.5 | 154 | C | 120.8 | 1.5 |
| | | 154 | D | 197.9 | 2.4 |
| 4 | 1-1.5 | 138 | D | 202.0 | 2.4 |
| 5 | 1-1.5 | 138 | C | 94.7 | 1.1 |
| | | 134 | D | 181.7 | 2.2 |
| 6 | 1-1.5 | 156 | D | 232.5 | 2.8 |
| 7 | 2-2.5 | 211 | C | 73.2 | 0.9 |
| | | 210 | D | 170.9 | 2.2 |
| 8 | 2-2.5 | 229 | C | 69.3 | 0.9 |
| | | 225 | D | 174.6 | 2.2 |
| 9 | 2-2.5 | 204 | D | 156.0 | 2.0 |
| 10 | 2-2.5 | 197 | D | 106.3 | 1.3 |
| | | 196 | C | 96.9 | 1.2 |
| 11 | 1-1.5 | 147 | D | 147.1 | 1.8 |
| 12 | 1-1.5 | 174 | C | 152.7 | 1.9 |
| **Mean (s.d.)** | **1 YO** | | **C** | **122.5 (20.6)** | **1.5 (0.3)** |
| | | | **D** | **188.5 (29.3)** | **2.3 (0.3)** |
| | **2 YO** | | **C** | **79.8 (14.9)** | **1.0 (0.2)** |
| | | | **D** | **152.0 (31.5)** | **1.9 (0.4)** |
| | **All seals** | | **C** | **106.5 (28.2)** | **1.3 (0.3)** |
| | | | **D** | **175.2 (33.9)** | **2.1 (0.4)** |

**Table 2.3. Comparison of mean values (s.d.) of various diving behaviors during directed transit across the bay for seals swimming under the control and drag treatments (grey shading).** Behaviors are described in the text. Results are based on mixed effect models described in the text. Asterisks denote significant differences between treatments in the following order: **$p < 0.01$, *$p < 0.05$.

| | Diving Behavior | | | | | |
|---|---|---|---|---|---|---|
| **Treatment** | **Ascent rate ($m\ s^{-1}$)** | **Bottom time : Dive duration** | **Descent rate ($m\ s^{-1}$)** | **Dive duration (s)** | **Maximum depth (m)** | **Surface Interval (s)** |
| **Control** | 0.95 | 0.55 | 0.89 | 1083 | 266 | 102 |
| | (0.11) | (0.06) | (0.12) | (123) | (43) | (11) |
| **Drag** | 0.82 | 0.55 | 0.80 | 1196 | 254 | 149 |
| | (0.19) | (0.07) | (0.12) | (278) | (56) | (44) |
| **All** | 0.89* | 0.55 | 0.84* | 1139 | 260 | 125** |
| | (0.16) | (0.06) | (0.13) | (216) | (49) | (39) |

**Table 2.4. Comparison of mean values (s.d.) of dive ascent and descent behaviors for three seals swimming under both the control and drag treatments (grey shading) with accelerometers.** Behaviors are described in the text. There was a tendency for decreased swim speeds and shallower pitch angles during descent under the drag treatment, although these results were not statistically significant (paired Students t-tests, $p$ = 0.06 and 0.12, respectively). "Relative drag" is a drag multiplier, if optimal swim speed is proportional to $(\text{BMR/drag})^{1/3}$.

| | | Ascent | | | | Descent | | | |
|---|---|---|---|---|---|---|---|---|---|
| **Seal** | **Treatment** | **Pitch (degrees)** | **Vertical rate (m/s)** | **Swim speed (m/s)** | **Relative drag** | **Pitch (degrees)** | **Vertical rate (m/s)** | **Swim speed (m/s)** | **Relative drag** |
| 7 | C | 29.0 (18.1) | 1.11 (0.34) | 1.51 (1.13) | | -41.0 (25.6) | 1.04 (0.25) | 1.49 (1.06) | |
| | D | 24.2 (20.5) | 0.83 (0.21) | 1.46 (1.10) | 1.06 | -32.9 (28.6) | 0.89 (0.21) | 1.47 (1.09) | 0.99 |
| 8 | C | 15.8 (24.3) | 0.88 (0.29) | 1.36 (1.00) | | -30.0 (28.2) | 0.79 (0.14) | 1.38 (1.02) | |
| | D | 15.0 (11.4) | 0.41 (0.06) | 1.19 (0.98) | 1.55 | -25.9 (29.9) | 0.51 (0.10) | 1.22 (0.94) | 1.48 |
| 10 | C | 21.6 (17.8) | 0.87 (0.19) | 1.63 (1.11) | | -33.7 (27.3) | 0.89 (0.16) | 1.61 (1.14) | |
| | D | 27.2 (19.2) | 0.89 (0.21) | 1.72 (1.18) | 0.87 | -34.2 (24.8) | 0.81 (0.15) | 1.54 (1.09) | 1.33 |
| **Mean (s.d.)** | **C** | **22.2 (6.6)** | **0.95 (0.14)** | **1.50 (0.14)** | | **-34.9 (5.6)** | **0.91 (0.13)** | **1.49 (0.12)** | |
| | **D** | **22.1 (6.3)** | **0.71 (0.26)** | **1.46 (0.27)** | **1.16** | **-31.0 (4.5)** | **0.74 (0.20)** | **1.39 (0.14)** | **1.27** |

**Table 2.5. Comparison of estimations of the total number of flipper strokes for each seal under each treatment (D = drag, C = control) during the entire measurement period.** Strokes (a) includes the number of strokes measured directly from accelerometers; (b) includes values calculated based on the relationship between time at sea and total number of flipper strokes (eq. 2.2 in text); (c) includes values calculated based on a constant flipper stroking frequency of 1459 strokes $h^{-1}$, as presented in the text. Error columns represent percent differences in number of strokes estimated using the different approaches – for example, the Error (a-c) column represents the percent difference in strokes estimated between measured values and values calculated using a constant stroking frequency of 1459 strokes $h^{-1}$. The mean (s.d.) error of each pairwise comparison is included below each error column.

| Seal | Treatment | Strokes (A) | Strokes (B) | Strokes (C) | Error (A-B) | Error (A-C) | Error (B-C) |
|---|---|---|---|---|---|---|---|
| 1 | C | | 58665 | 61513 | | | -4.85 |
| | D | | 89407 | 88921 | | | 0.54 |
| 2 | D | | 104590 | 102457 | | | 2.04 |
| | C | | 79052 | 79689 | | | -0.81 |
| 3 | C | | 77362 | 78182 | | | -1.06 |
| | D | | 93350 | 92436 | | | 0.98 |
| 4 | D | | 789236 | 712849 | | | 9.68 |
| 5 | C | | 132704 | 127522 | | | 3.90 |
| | D | | 213878 | 199892 | | | 6.54 |
| 6 | D | | 247062 | 229477 | | | 7.12 |
| | C | | 47291 | 51372 | | | -8.63 |
| 7 | C | 73935 | 63118 | 65483 | 14.63 | 11.43 | -3.75 |
| | D | 40017 | 37741 | 42858 | 5.69 | -7.10 | -13.56 |
| 8 | C | 90292 | 93914 | 92939 | -4.01 | -2.93 | 1.04 |
| | D | 42478 | 37633 | 42762 | 11.41 | -0.67 | -13.63 |
| 9 | D | 26822 | 24301 | 30876 | 9.40 | -15.11 | -27.06 |
| 10 | D | 236420 | 275980 | 255259 | -16.73 | -7.97 | 7.51 |
| | C | 51308 | 42194 | 46828 | 17.76 | 8.73 | -10.98 |
| 11 | D | 110902 | 126561 | 122045 | -14.12 | -10.05 | 3.57 |
| 12 | C | 433514 | 404180 | 369554 | 6.77 | 14.75 | 8.57 |
| **Mean algeb. error (s.d.)** | | | | | **3.42 (12.3)** | **-0.99 (10.4)** | **-1.64 (9.3)** |
| **Mean absol. error (s.d.)** | | | | | **11.17 (5.0)** | **8.75 (4.8)** | **6.79 (6.3)** |

# Chapter 3

# Summing the strokes: extreme energy economy in a large marine carnivore

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## Abstract

The energy requirements of free-ranging marine mammals are challenging to measure due to elusive and far-ranging feeding habits, but are important to quantify given the potential impacts of these high-level predators on prey resources and marine ecosystems. Given their large body size and carnivorous lifestyle, we would predict that northern elephant seals (*Mirounga angustirostris*) have elevated field metabolic rates (FMRs) that require high prey intake rates, especially during pregnancy. Disturbance associated with climate change or human activity is predicted to further elevate energy requirements due to an increase in locomotor costs required to accommodate a reduction in prey or time available to forage. We determined FMRs, total energy requirements, and the relative partitioning of ingested energy among competing demands for 20 adult female elephant

seals. We constructed energy budgets by coupling measurements of foraging success (energy gain) with experimental measurements of locomotion costs in free-swimming seals. Body size, time spent at sea and reproductive status strongly influenced FMR. During the short foraging migration, FMR averaged 73.6 (± 3.9) kJ kg$^{-1}$ d$^{-1}$ – only 10% greater than predicted basal metabolic rate. During the long migration, when seals were pregnant, FMRs averaged 56.1 (± 5.6) kJ kg$^{-1}$ d$^{-1}$ – values below those predicted to be necessary to support basal metabolism in mammals of this size. Low FMRs in pregnant seals were driven by hypometabolism coupled with a positive feedback loop between improving body condition and reduced flipper stroking frequency. In contrast, three additional seals carrying large, non-streamlined instrumentation saw a four-fold increase in energy partitioned toward locomotion, resulting in elevated FMRs and only half the mass gain of normally-swimming study animals. These results highlight the importance of keeping locomotion costs low for successful foraging in this species. In preparation for a costly lactation period, female northern elephant seals utilize a foraging strategy of extreme energy economy whereby energy savings from reduced locomotion and basal metabolism costs are shuttled towards growth, gestation, and fat storage. Remarkably, the energy, and therefore prey, requirements of this high-level predator are 75-85% lower than for similarly-sized terrestrial carnivores, and only half those of other marine mammals.

## List of symbols used

| | |
|---|---|
| ADL | aerobic dive limit |
| cADL | calculated aerobic dive limit |
| BMR | basal metabolic rate (kJ $kg^{-1}$ $d^{-1}$) |
| DAS | time spent at sea ($d^{-1}$) |
| DG | drag treatment; refers to seals carrying added drag during their shorter foraging migration |
| DMR | diving metabolic rate (kJ $kg^{-1}$ $d^{-1}$) |
| FMR | mass-specific field metabolic rate (kJ $kg^{-1}$ $d^{-1}$) |
| FMR* | absolute field metabolic rate (kJ $d^{-1}$) |
| HIF | heat increment of feeding |
| LT | long trip; refers to seals during their longer foraging migration (pregnant) |
| R | stroke rate (strokes $d^{-1}$) |
| Sn | total number of strokes |
| ST | short trip; refers to seals during their shorter foraging migration (not pregnant) |
| TDR | time-depth recorder |

## 3.1 Introduction

Upper trophic level predators are important components of food webs, having disproportionate, landscape-level effects on the structure and function of ecosystems (Power et al., 1996; Worm et al., 2002; Duffy, 2003; Baum and Worm, 2009; Ripple et al., 2014). Reductions in many species of large marine carnivores, including marine mammals, sharks and piscivorous fishes, have prompted calls for effective ecosystem-based management targeted at recovering depleted populations, while proactively protecting intact populations from decline (Jackson et al., 2001; Pauly et al., 2002; Baum et al., 2003; Worm et al., 2003; Pikitch et al., 2004; Reynolds III, 2005; Olsen et al., 2006). As a result, many studies have focused on describing the distributions and foraging success of these groups in relation to habitat features (e.g., Costa et al., 2010; Block et al., 2011; Robinson et al., 2012) and prey distributions (e.g., Merrick et al., 1997; Goetz et al., 2007) with little information available on the basic resource needs of these species. In contrast to many terrestrial systems, this information is difficult to come by for marine animals because they forage at sea, making their food habits and foraging behaviors challenging to directly measure. Yet assessing the prey requirements of high-level marine predators is central to determinations of how resilient they might be to ongoing anthropogenic disturbance and rapid environmental change.

In general, marine mammals have large energy requirements that are thought to be driven by the relatively large metabolic demands prescribed by carnivory (McNab, 1986a; Nagy, 1987) and the maintenance of a high core body temperature in water (Dejours, 1987; Speakman and Król, 2010; Hudson et al., 2013). Foraging effort will reflect these requirements, and will contribute to energetic demands via the costs associated with locating, chasing and capturing prey (Stephens and Krebs, 1986; Krebs and Davies, 2009). To remain in positive energy balance, the energy acquired from foraging must exceed the energetic cost of foraging (Boyd, 2002). More successful foragers will accumulate surplus energy to allocate towards growth and reproduction, and thus, a high foraging efficiency via minimization of energy expenditure is expected to be adaptive for all animals, and especially for predators with large energy requirements. Marine animals can minimize locomotion costs by adoption of stereotyped, energy-saving swimming behaviors such as drift diving (Crocker et al., 1997; Webb et al., 1998b; Nowacek et al., 2001), burst-and-glide swimming (Skrovan et al., 1999; Williams et al., 2000), and wave-riding (Williams et al., 1992). The disruption of these routine behaviors can be predicted to increase the amount of time and energy spent foraging, resulting in increased locomotory costs, thereby reducing foraging success.

The ecology of the northern elephant seal, *Mirounga angustirostris*, (Fig. 3.1) facilitates acquisition of foraging behavior data using archival tagging instrumentation, making it an ideal study species to address questions on the effects of disturbance on the foraging success of marine carnivores. Every year, adult females return to land for one month in between each of two foraging migrations, once to birth and nurse a pup, and once to molt their pelage (Le Boeuf et al., 2000). Females are inseminated just prior to weaning, and then return to sea to forage for 2-2.5 months before hauling out for the molt. Implantation likely occurs during or after the molt, when seals return to sea for 7-8 months to forage and gestate the fetus. The demands for foraging success are considerable during this time, as pregnant seals must ingest sufficient energy to replace what was lost during the molt as well as store sufficient energy reserves to support the fasting mother and her suckling pup during the costly month-long lactation period (Costa and Gentry, 1986; Crocker et al., 2001).

Our objectives in this study were to determine the total energy requirements, and the relative partitioning of energy among competing demands, for adult female northern elephant seals under normal foraging conditions. We compare these data to those from 3 seals encountering increased foraging costs due to increased drag. To achieve this, we constructed complete energy budgets by coupling measurements of foraging success (energy gain) during each foraging migration with experimental measurements of locomotion costs in free-swimming seals (Maresh et al., 2014). For one of the largest predators in the northern Pacific Ocean, we describe (1) increased energy economy as a function of pregnancy and/or time spent at sea; (2) strong, predictive relationships between body size, flipper stroking mechanics, and at-sea energy expenditure; and (3) reduced foraging success resulting from the disruption of stereotyped, energy-saving swimming behaviors.

## 3.2 Methods

### 3.2.1 Flipper stroking data

22 adult female elephant seals were instrumented at their breeding colony in the Año Nuevo State Reserve, California, USA (37º 5’ N, 122º 16’ W) from 2009 – 2013. Healthy seals were randomly selected and 15 were of known age ranging from 5 to 12 years old. One seal, N796, was instrumented in both 2009 and 2010. The study included both annual foraging migrations: the short post-breeding migration (February through April; N = 16) and the long post-molting gestational migration (June through December; N = 7).

We chemically immobilized the seals for instrument attachment and recovery using established protocols (Le Boeuf et al., 1988; Le Boeuf et al., 2000). Seals were instrumented with a time-depth recorder (TDR) (Wildlife Computers MK9, MK10; or Lotek, St. John's, NL, Canada: 2310) and a tri-axis accelerometer/magnetometer (Wildlife Computers MK10-style prototype, 16-Hz sampling rate, N = 9, sample years 2009 – 2011; or Little Leonardo ORI2000-D3GT, 32-Hz sampling rate, N = 14, sample years 2011 – 2013) for collection of at-sea diving and flipper stroking data, respectively. The raw time-series of accelerometry measurements were truncated according to departure/arrival times identified using the diving record, and flipper strokes isolated using one of two custom-written programs in Igor Pro 6.22A (WaveMetrics, Inc., USA), depending on the instrument model used. In brief, side-to-side flipper movements were detected as fluctuations in the transverse axis – “swaying” acceleration – and the static (positional) component was separated from the dynamic (movement) component using a 1-Hz low-pass filter (Sato et al., 2003; Mitani et al., 2010; Maresh et al. 2014). The remaining peaks and troughs in the dynamic swaying acceleration with amplitudes greater than 1 m $s^{-2}$ were considered to be individual flipper strokes and were used in analyses.

Output from the Wildlife Computer instruments included raw acceleration data, and a user-written algorithm was used to identify and count individual flipper strokes (Maresh et al., 2014). In contrast, with the exception of 12 hours per record, raw data were not output from the Little Leonardo instruments – instead, output included stroke counts as the algorithm for identifying strokes from the raw data was built into the instruments. To make comparisons between algorithms, we processed each seal’s 12 hours of raw Little Leonardo accelerometry data through our user-written algorithm and used the percent discrepancy between stroke counts to correct the total number of counts output by the Little Leonardo algorithm. In most cases, the total number of strokes counted by the two algorithms were within 10% of each other; however, in two cases, the discrepancy was greater than 10% (14% for T35, 20% for T730). For this reason, and for consistency, we used corrected counts from the Little

Leonardo instruments, rather than the processed output from the instruments, in analyses.

As part of a separate study, three seals were additionally outfitted with prototype acoustic tags, for testing of their viability in future studies. The tags were not deployed with the intention of affecting the foraging success of the animals, but upon recovery these seals were undersized and clearly nutritionally stressed, probably due to the added hydrodynamic drag imposed on the animals by the bulky, non-streamlined instruments. We include these individuals in our analyses here to determine how foraging success and efficiency is affected by disturbance to routine swimming behaviors via increased locomotory costs.

### 3.2.2 Energetics data

The surplus energy available to a seal for production of new tissue (growth, fat storage, gamete production, fetal gestation, etc.) is a function of the difference between gross food energy ingested at sea and energy expended while foraging, and can be described by the equation:

$$E_{\mathrm{PRODUCTION}} = E_{\mathrm{INGESTED}} - E(\mathrm{Feces} + \mathrm{Urine} + \mathrm{Digestion} + \mathrm{Maintenance} + \mathrm{Locomotion}) \quad (3.1)$$

where some energy from ingested prey items is lost in the production and excretion of feces and urine, as well as in the fuelling of digestion costs

(Lavigne et al., 1985; Costa, 2012), basal maintenance metabolism and locomotion.

To estimate surplus energy gained from foraging (i.e., spent in production), we measured the mass of each seal at the beginning and end of each trip by suspension in a canvas sling from a tripod using a Dyna-Link scale (1,000 +/- 1 kg). Mass at departure and upon arrival was corrected for any time spent on land after instrument attachment or before instrument retrieval, respectively, using an equation derived from serial mass measurements of fasting female seals (Simmons et al., 2010). For seals returning from their long, post-molt migrations (i.e., during the breeding season), the mass of the pup was added to that of the mother five days post-parturition. Adipose and lean tissue gain was estimated from mass change and body composition, assuming that the five-day-old pup was 13% adipose tissue (Crocker et al., 2001). Energy gain was estimated assuming that adipose tissue was 90% lipid, and lean tissue was 27% protein with a gross energy content of 39.33 kJ $g^{-1}$ for lipids and 23.5 kJ $g^{-1}$ for protein (Crocker et al., 2001). Additional gestation costs associated with maternal metabolism were assumed to be negligible based on previous research on other capitally-breeding phocids (Hedd et al., 1997; Sparling et al., 2006), and so were not added to the energy budget of seals in this group.

To estimate energy expenditure during the foraging migrations (i.e., not spent in production), we used an equation relating total field metabolic rates (FMRs) to total number of swim strokes in free-swimming, non-reproductive, fasting seals [$E_{EXPEND}$ (J $kg^{-1}$) = 2.58Sn, where Sn is the number of flipper strokes (Maresh et al., 2014)]. Due to the high sampling frequency of accelerometers, it was common for the battery life of the instrument to expire before the seal had returned to shore; in these cases (N = 10), we extrapolated $E_{EXPEND}$ on a per-day basis to the total time spent at sea as measured by the time-depth recorder.

Total energy expenditure, $E_{EXPEND}$ , represents the sum of all component costs (E(Feces + Urine + Digestion + Maintenance + Locomotion) from eq. 3.1), and we estimate each separate cost and its relative contribution to total energy expenditure using values and equations from previous studies. Lavigne et al. (1982) estimated that phocid seals lose approximately 9-10% of gross energy from prey as feces and 7-8% of the remaining energy as urine, which leaves approximately 83% of gross energy from prey as metabolizable energy. We used this value for assimilation efficiency in elephant seals, which is in line with studies on other phocids where metabolizable energy was measured as 88.6% and 86.6% of gross energy in ringed (Parsons, 1977) and harp seals (Keiver et al., 1984), respectively, and shown to range from between 78.3-91.6% in pinnipeds, depending on the diet (Costa and William, 1999). To account for digestion costs (the heat increment of feeding (HIF)), we used the estimate of 11.6% of metabolizable energy measured in juvenile elephant seals (range = 6.4-18%) (Barbour, 1993). This value is in close agreement with other studies of HIF in marine mammals: 10-13% in sea otters (Costa and Kooyman, 1984), 10-17% in harp seals (Gallivan and Ronald, 1981; Lavigne, 1982), and 5.5% in harbor seals (Ashwell-Erickson and Elsner, 1981).

As basal metabolic rate (BMR) has not been measured for adult female elephant seals, we used Kleiber's (1975) predictions of BMR for terrestrial mammals to estimate the maintenance costs of the seals in this study. Kleiber values are in agreement with previous measurements on quiescent, submerged pinnipeds (Hurley and Costa, 2001; Williams et al., 2004a).

Finally, after accounting for assimilation efficiency, HIF and basal metabolism, any remaining costs from $E_{EXPEND}$ were assumed to represent energy spent on locomotion. With all costs and surplus energy spent in production accounted for, we could then estimate the energy ingested from prey that is necessary to balance each seal's energy budget.

### 3.2.3 Statistical analysis

The influence of body size, time at sea and foraging migration (short or long trip) on field metabolic rate, locomotion costs and flipper stroking frequency, was investigated using multiple linear regression (MLR) models. Candidate models included the interaction term body size x migration to test whether the effect of body size on each of the response variables was dependent on the migration, in which case we ran MLR models on each of the migrations separately. These MLRs included the potential interaction between time at sea and body size. Generalized least squares (GLS) models with fixed variance structure were used to test for the influence of body size and foraging migration on the proportion of ingested energy allocated towards growth and towards locomotion costs. All means are expressed as (±

s.d.), and results were considered statistically significant when $p < 0.05$, and potentially biologically relevant when $p < 0.10$. Analyses were performed using the built-in ‘lm’ function, and the ‘gls’ function of the ‘nlme’ package in R 2.15.3 (R Development Core Team, 2013). All model combinations were fitted with best model fits based on the lowest Akaike information criteria corrected for small sample size (AICc).

## 3.3 Results

### 3.3.1 Energy expenditure

Energy expenditure for each of the 23 seals carrying accelerometers is listed in Table 3.1. For each of the variables discussed below – field metabolic rates (FMRs), locomotion costs, and flipper stroking frequency – the response was influenced by the interaction between body size and foraging migration (short or long trip) (MLR results, $p < 0.05$ for each), so we ran MLRs on each of the migrations separately. As described below, our data indicate that, in general, locomotion behavior and the resulting field energetics of seals were most influenced by time spent at sea during the short trip, and the animal’s mass during the long trip.

FMRs were higher during the short trip (73.6 ± 3.9 kJ $kg^{-1}$ $d^{-1}$) than during the long trip (56.1 ± 5.6 kJ $kg^{-1}$ $d^{-1}$), with a weak effect of body size such that the largest seals expended the least amount of energy on a mass-specific basis during the longer foraging migration (Fig. 3.2). In other words, pregnant seals had lower mass-specific FMRs for a given size, falling below Kleiber predictions of mammalian basal metabolic rates (Table 3.1, Fig. 3.3). FMR in this group could be described by the equation:

$$\mathrm{FMR}_{\mathrm{LT}} = 2592\mathrm{M}^{-0.64} \quad (r^2 = 0.53,\ F_{1,5} = 5.673,\ p = 0.06) \qquad (3.2)$$

where $\mathrm{FMR}_{\mathrm{LT}}$ is field metabolic rate during the long trip in kJ kg$^{-1}$ d$^{-1}$, and M is mass in kg. FMR during the long trip was not affected by time spent at sea ($p = 0.89$).

At-sea FMRs of the smallest, short migration (i.e., non-pregnant) seals were as much as 1.3 times Kleiber predictions of BMR, suggesting increased energy economy during pregnancy, and particularly so in larger seals. In contrast to seals during the long trip, FMR during the short trip was not affected by mass ($p = 0.38$), but instead was affected by time spent at sea according to the equation:

$$\mathrm{FMR}_{\mathrm{ST}} = 8.2t^{0.51} \quad (r^2 = 0.33,\ F_{1,11} = 5.428,\ p = 0.04) \qquad (3.3)$$

where $\mathrm{FMR}_{\mathrm{ST}}$ is field metabolic rate during the short trip in kJ kg$^{-1}$ d$^{-1}$, and $t$ is time spent at sea in days. However, with the mass term removed from FMR, energetic expenditure on a per day basis was significantly affected by mass during the short trip according to the following equation:

$$\mathrm{FMR}^{*}_{\mathrm{ST}} = 144.6\mathrm{M}^{0.89} \ (r^2 = 0.82,\ F_{1,11} = 51.23,\ p < 0.001) \qquad (3.4)$$

where $FMR^{*}_{ST}$ is field metabolic rate during the short trip in kJ $d^{-1}$, and M is mass in kg (Fig. 3.3). FMR of seals during the long trip was not similarly affected ($p = 0.24$).

With basal costs (Kleiber, 1975) removed, the impact of each flipper stroke on locomotion costs was higher during the short trip (0.24 ± 0.13 J $kg^{-1}$) than during the long trip (-0.41 ± 0.26 J $kg^{-1}$). However, it is likely that basal metabolism during the long trip was actually suppressed because of pregnancy (Renouf and Gales, 1994; Hedd et al., 1997; Sparling et al., 2006; Ochoa-Acuna et al., 2009) or extended time at sea (Hassrick et al., 2010; Vazquez-Medina et al., 2011), rather than that locomotory costs were negative, and so we limit further consideration of locomotory costs to those given the assumption of hypometabolism (see discussion).

Flipper stroking frequency was 24% lower during the long migration (21725 ± 2159 strokes $d^{-1}$) than during the short migration (28538 ± 1522 strokes $d^{-1}$) (Welch two-sample t-test, $t = -9.7674$, $df = 7.471$, $p < 0.001$) (Fig. 3.4). There was a weak effect of body size during the long migration such that larger, pregnant seals stroked less (Table 3.1). Stroking frequency for seals during the long migration was described by the equation:

$$R_{LT} = 1{,}004{,}616M^{-0.64} \quad (r^2 = 0.53,\ F_{1,5} = 5.673,\ p = 0.06) \qquad (3.5)$$

where $R_{LT}$ is flipper stroke rate of seals during the long foraging trip in strokes $d^{-1}$, and M is mass in kg. Note that the summary statistics are the same as those for eq. 3.2 as FMR was calculated from flipper strokes. In contrast to these results, there was no effect of body size on flipper stroking frequency during the short trip ($p$ = 0.38); there was, however, an effect of time spent at sea on stroke rate in this group, which is described by the equation:

$$R_{ST} = 3164t^{0.51} \quad (r^2 = 0.33,\ F_{1,11} = 5.428,\ p = 0.04) \qquad (3.6)$$

where $R_{ST}$ is flipper stroke rate of seals during the short foraging trip in strokes $d^{-1}$, and $t$ is time spent at sea in days. Note that the summary statistics are the same as those for eq. 3.3 as FMR was calculated from flipper strokes.

### 3.3.2 Foraging success and energy budgets

Mass gain, energy gain, and other indicators of foraging success for each seal are listed in Table 3.2. This information was used in combination with energetic expenditures calculated above to determine the overall energy budget of each seal during her respective foraging migration (Fig. 3.5). The proportion of total energy intake partitioned towards growth of the adult seal was the same during both migrations (32.0 ± 6%) (GLS with fixed variance structure, $p$ = 0.37), with no effect of mass on this partitioning (GLS with fixed variance structure, $p$ = 0.26). During the long foraging trip, seals were able to devote an additional 4% of total energy intake to fetal growth by reducing basal metabolism and locomotion costs: from 38% and 3.8% to 35% and 2.9%, respectively (Fig. 3.5).

In contrast to growth costs, the proportion of total energy intake utilized in locomotion differed between the two migrations (GLS with fixed variance structure, $r^2 = 0.77$, $F_{2,17} = 28.03$, $p < 0.001$), with no effect of body mass ($p = 0.81$) such that the proportional allocation of total energy toward locomotion tended to be less during the long trip (-6.9 ± 4.0%) than during the short trip (3.8 ± 2.3%). Again, these values tended to fall below Kleiber predictions of mammalian BMR during the long trip, but it is likely that this result is an artifact of inflated BMR predictions – it is more likely that seals are hypometabolic during the long migration and thus Kleiber predictions are actually an overestimate for this group, rather than that locomotion costs are zero or negative (Maresh et al., 2014) (see discussion). Assuming the energetic cost of each flipper stroke is the same for seals during both migrations, and because seals stroke 24% less during the long migration (Fig. 3.4), we can estimate the actual proportion of total energy intake allocated towards locomotion in this group to be about 2.9%. Fetal gestation costs consumed approximately 4% of total energy expenditure during the long trip; to “balance the budget,” energy must have been shuttled away from metabolic overhead, which would require an approximately 21 ± 6.5% reduction in BMR to achieve (Fig. 3.5).

### 3.3.3 Seals with added drag

Seals swimming with added drag during the short migration (hereafter referred to as “drag seals,” N = 3) experienced a 22% increase in FMR (Table 3.1, Fig. 3.2), resulting in half the mass gain (i.e., foraging success) of other short-trip seals swimming without the experimental tags (hereafter referred to as “normally-swimming seals”) (Table 3.2). However, this should be interpreted as a conservative estimate of energy expenditure in the drag group as we have assumed stroking costs similar to those of normally-swimming seals. Two of the drag seals foraged at sea for as long as normally-swimming short-trip seals (74.6 ± 4.8 days), but with substantially lower foraging success. The remaining drag seal (1234) spent 33% more time foraging at sea (100.8 days) than normal, with below normal foraging success results intermediate between those of the other two drag seals (Table 3.2).

Poor foraging success in the drag seals was the result of abnormal partitioning of energy intake between locomotion and growth costs. Drag seals spent more than four times as much energy on locomotion (16.7 ± 3.3% of total energy intake) as the normally-swimming, short-trip seals reported above, with a resultant one-third of the energy spent on growth (11.7 ± 5.3% of total energy intake) (Fig. 3.5). This was likely due to increased locomotion costs associated with overcoming the added hydrodynamic drag during diving and swimming, which is supported by the increased flipper stroking frequency demonstrated by the drag seals in comparison to normally-swimming, short-trip seals (22.4% more strokes per day) (Fig. 3.4). The limited variation in stroking frequency for drag seals compared to the other groups suggests these individuals may have been pushing against a biomechanically-constrained upper limit to swimming effort while foraging.

## 3.4 Discussion

### 3.4.1 Energy economy and the effects of pregnancy

The energy requirements of adult female northern elephant seals are much lower than those described for other carnivores, and particularly so during pregnancy. Mammalian carnivores typically have higher energy needs than other terrestrial mammals, and thus require large food supplies to fuel fast metabolisms (McNab, 1986a; Nagy, 1987). As such, FMRs tend to run high in this group, ranging from 1.99 – 4.65 times Kleiber (1975) predictions of BMR in terrestrial mammalian carnivores (summarized in Nagy et al., 1999; Nagy, 2005), and from 4.88 – 6.44 Kleiber predictions in marine mammal carnivores (Reilly and Fedak, 1991; Nagy, 1994) (although see Costa and Trillmich, 1988). However, more recent studies on the diving metabolism (DMR) of adult phocid seals indicate increased metabolic efficiency in this group compared to other marine carnivores, with DMRs of captive grey seals measured as 1.41 – 2.18 Kleiber (Sparling and Fedak, 2004) and DMRs of wild, free-swimming Weddell seals measured as 1.3 – 3.5 Kleiber (Williams et al., 2004a). In this last example, DMRs in Weddell seals were dependent on dive duration, resulting in 1.7 Kleiber for seals diving for as long as the average dive duration of elephant seals in our study (21.5 min). Captive studies on newly weaned northern elephant seal pups (approximately 1.5-2.5 months old) have measured metabolic rates of 0.9-1.4 Kleiber during submergence (Noren, 2002; Houser et al., 2012; Tift et al., 2013), suggesting the capability for diving hypometabolism in even the youngest elephant seals.

During the 2- to 2.5-month post-breeding foraging trip, adult elephant seals were able to recover the energy reserves lost during lactation by operating at only 1.10 (range = 1.00 – 1.20) times Kleiber predictions of basal metabolism, indicating extreme metabolic efficiency in this species (Table 3.1, Fig. 3.3). These results are in line with Meir et al.'s (2009) short-term study on blood-oxygen depletion in free-swimming juvenile elephant seals, where large oxygen storage capacities combined with a high tolerance for hypoxia indicated these animals should be able to operate aerobically at 1.22 – 1.32 times Kleiber predictions. Our values are also within the range (0.99 – 1.31 Kleiber) of metabolic rates measured in juvenile elephant seals diving in a metabolic chamber (Webb et al., 1998a), and in wild, free-swimming juvenile elephant seals (0.88 – 1.89) (Maresh et al., 2014). While measurements in these examples were from juvenile animals, recent studies on other phocid seals in captivity were unable to detect a difference between juvenile and adult DMRs (e.g., grey seals: Sparling and Fedak, 2004) or BMRs (e.g., harp harbor and ringed seals: Ochoa-Acuna et al., 2009), suggesting that using measurements of metabolism in juveniles to ground truth our calculations for adults is a valid approach.

The degree of metabolic efficiency was correlated with body size and reproductive status, with the largest animals having the lowest mass-specific FMRs during pregnancy (Fig. 3.2). During the 7- 8-month post-molt foraging trip, female seals were able to fuel the costs associated with fetal gestation and an 88% (± 19%) increase in body size by operating at FMRs falling below Kleiber predictions of basal metabolic rates (Fig. 3.3). In most mammals, pregnancy elevates metabolic rates (Brody, 1945; Gittleman and Thompson, 1988); however, like other phocids, female elephant seals fast during the breeding season and therefore must fuel energetically expensive lactation costs using only onboard fuel reserves accumulated during the post-molt (long duration) foraging trip. Suppressed metabolism and increased fuel economy during pregnancy is likely a pre-pupping fattening strategy, and while it has been measured in resting, captive harp seals (Renouf and Gales, 1994; Hedd et al., 1997; Ochoa-Acuna et al., 2009), grey seals (Sparling et al., 2006), harbor and ringed seals (Ochoa-Acuna et al., 2009), our study is the first to demonstrate suppressed metabolism during pregnancy in actively foraging, wild seals during their months-long migrations.

Our results provide empirical support for hypotheses regarding hypometabolism in female northern elephant seals based on diving behavior. Occasionally during the short post-breeding foraging trip, and regularly during the long post-molt trip, seals dive past their calculated aerobic dive limit (cADL) (Le Boeuf, 1994), a theoretical dive duration threshold beyond which a breath-holding animal would rapidly accumulate the metabolic by-products associated with a switchover to anaerobic metabolism (Kooyman et al., 1980). Fuelling a dive anaerobically requires a recovery period afterward, when metabolites are cleared and oxygen stores are replenished. During recovery, seals are unable to dive, precluding them from foraging, and so an increase in the time spent diving aerobically would be expected to be at a premium for any animal who must locate and capture prey while in breath-hold (Kooyman et al., 1980). A diving animal's true ADL depends on the size of the oxygen stores available to it during breath-hold and the rate at which it depletes those stores at depth, while its calculated ADL depends on our estimates of those parameters. Previous authors have suggested that because female elephant seals are consistently diving past their cADLs without the expected concomitant recovery period following, traditional predictions of diving metabolic rates based on allometric equations must be overestimates – instead, elephant seals must be hypometabolic while diving, and particularly so during the long foraging trip (Le Boeuf et al., 1988; Kooyman, 1989; Hindell et al., 1992; Hassrick et al., 2010). Indeed, predictions of FMRs as low as 0.67 Kleiber during particularly long dives are in agreement with our average value of 0.85 (± 0.07) Kleiber across all dive durations in this group. Compared to similarly-sized short-trip females, who are themselves operating at remarkably low metabolic rates (this study), long-trip seals were shown to suppress their field metabolism by a further 23% (range = 17% in smaller seals to 34% in the largest), to rates below those predicted to be necessary to support even basic maintenance metabolism

(Fig. 3.3). Boyd (2002) predicted this trend for marine mammals using first principles, arguing that thermoregulation costs are lower in larger animals, and that locomotion becomes increasingly more efficient with body size in aquatic animals; however, he predicted the convergence of marine mammal FMR with terrestrial mammal BMR at body sizes an order of magnitude larger than those of the elephant seals in this study.

Lower at-sea FMRs in seals during pregnancy were also the result of reduced flipper stroking frequencies (Fig. 3.3), with seals stroking 24% slower than those during the short trip (approximately 15 and 20 strokes min$^{-1}$, respectively). For both groups, most flipper stroking occurs during the ascent phase of the dive cycle (Fig. 3.7), when seals must work against their negative buoyancy at depth to reach the surface (Davis et al., 1999; Sato et al., 2003). As the foraging migration progresses, seals are able to store more fat, becoming less negatively buoyant as a result (Crocker et al., 1997; Webb et al., 1998b; Adachi et al., in review), and we would expect an inverse relationship between buoyancy and the number of flipper strokes required to surface (Watanabe et al., 2006; Aoki et al., 2011; Miller et al., 2012). However, seals remain overall negatively buoyant, which allows them to still passively glide during most of the descent (Adachi et al., in review). Seals generally gain more adipose tissue during the long trip (Table 3.2) and thus would be expected to be less negatively buoyant than their short-trip counterparts, reducing the number of flipper strokes necessary to surface. With each flipper stroke having a predictable effect on overall energy costs, this reduced stroking frequency results in approximately 1618 ± 674 MJ in energy savings across the long foraging migration. This energy economy in pregnant seals reduces by almost 29 days the time at sea needed to support measured foraging success, which has important implications for the synchronized timing of the breeding season in this species.

### 3.4.2 Energy budgets

Despite the 5-month difference in trip duration, partitioning of ingested energy was remarkably similar across the two migrations. Seals allocated approximately 68% and 64% of ingested energy towards work (digestion, basal maintenance and locomotion) during the short and long trips, respectively, and 32% towards the seal's own growth during both trips (Fig. 3.5). For pregnant seals, energy savings from suppression of basal metabolism and reduced flipper stroking freed up the additional 4% needed to fuel gestation costs.

During the short trip, locomotion costs were low, constituting approximately 4% of overall energy expenditure. This is somewhat lower than what has been reported for similarly-sized, freely-diving Weddell seals, where locomotory costs comprised approximately 8% of overall costs (calculated from eq. 3 in Williams et al. (2004a)). In contrast, locomotion costs of seals during the long migration were calculated as being negligible; however, this is likely the result of our assumption of an unvarying BMR equal to Kleiber predictions in these seals. As discussed above, several species of phocid seal have been shown to suppress their resting metabolisms during pregnancy in captivity (Renouf and Gales, 1994; Hedd et al., 1997; Sparling et al., 2006), and it is likely the case that elephant seals do the same. Indeed, Tift et al. (2013) were able to show that resting metabolic rate is suppressed in newly weaned elephant seals during breath-hold. It is likely that this hypometabolism is the driver of reduced at-sea FMRs in pregnant females rather than zero or negative locomotion costs. The physiological mechanism behind suppression is unclear, but may be a conditioning effect of chronic oxidative stress with increased time spent at sea (Hassrick et al., 2010; Vazquez-Medina et al., 2011). If locomotion costs on a per-stroke basis are instead assumed to be the same in pregnant seals as they are in non-pregnant seals, basal maintenance costs in pregnant elephant seals must be reduced by approximately 21% (range = 15 – 32%) of Kleiber predictions to “balance the budget” in terms of work costs (Fig. 3.5). This compares to a reported 30% and 27% reduction in the resting metabolism of captive, pregnant harp and grey seals, respectively (Hedd et al., 1997; Sparling et al., 2006), suggesting that the degree of metabolic suppression during pregnancy in phocids is modulated by activity levels.

Overall foraging success as determined by the net energy available to fuel production was highly variable for both migrations. We use the examples of short-trip seals U605 and U627 to illustrate this variability. These two seals were similar in age (5 YO) and body size (approximately 270 kg) prior to the 2012 post-breeding foraging migration, yet U627 had a 45% higher lipid mass gain than that of U605 (Table 3.2), representing a more than 2093 MJ difference in food ingestion between the two seals. Long-trip seals likewise showed variability in ingested food energy. Again, using an example to illustrate differences, seal 2036 was able to increase her body mass by 118%, and give birth to a 60 kg pup, compared to T730 who gave birth to a pup half the size, and increased her own body mass by only 66% while foraging during a similar time frame (2011 post-molt migration). However, 2036 was the fatter seal at the start of the migration (280 versus 257 kg) – being less negatively buoyant during the course of the trip would reduce locomotion costs as described above, freeing up more energy to devote towards production. Indeed, 2036 had a lower total number of flipper strokes despite a longer migration duration (Table 3.1). These results indicate a positive feedback loop in terms of foraging success, whereby increased ingestion of food energy increases adiposity, increasing buoyancy, which reduces overall locomotion costs, which in turn allows the seal to shuttle more ingested energy towards fattening.

### 3.4.3 Prey requirements

Based on the stomach contents of dead seals and on rare observations of prey capture, northern elephant seals are believed to be generalist feeders with a catholic diet that includes deep-water squid, Pacific herring and hake, myctophid fish, rockfish, bottom fish, lamprey and hagfish, various species of cartilaginous fish, and even bivalves, gastropods, and other shelled mollusks (Condit and Leboeuf, 1984; Antonelis et al., 1987). Size selectiveness in this species is unknown, so we assume average masses of prey species in estimating the number and capture rate of individual prey items; however, given a constant energy density specific to each diet item, our mass assumptions should not affect estimates of biomass removal for a particular prey species. With an understanding of energy expenditure during each of the foraging migrations, we can now estimate the amount of food stuffs required to fuel mass gain and gestation in adult female elephant seals.

Seals in this study ingested an average of 5020 (± 942) and 12,762 (± 1683) MJ during the course of the short and long migrations, respectively. This equates to approximately 125 (± 24) and 174 (± 39) MJ per day spent foraging. Our daily intake rate estimate for short-trip seals is in complete agreement with Sakamoto et al.'s (1989) estimate using an energy components analysis on the TDR record of one seal. Depending on the energy density of ingested prey items, elephant seals in both groups would have needed to capture approximately 3-15% of their average body mass in prey per day spent foraging, which is in close agreement with the 6.2% predicted by Le Boeuf et al. (1988). This ingestion rate is the equivalent of 10-40 kg of prey captured per day spent foraging at sea which is, again, in agreement with Le Boeuf et al.'s (1988) estimate of 20 kg based only on dive behavior. This ingestion rate is also the equivalent of 0.6-11.5 prey items per foraging dive (Fig. 3.6). Naito et al. (2013) reported 9.9-16.5 jaw opening events (prey capture attempts) per dive for four adult female northern elephant seals during their short foraging migrations; together with our results, this suggests that either not all capture attempts are successful, or that, as Naito et al. (2013) argue, elephant seals prey on smaller individuals than we assumed in our estimates here.

### 3.4.4 Disruption of routine foraging behaviors

The three seals carrying the experimental acoustic tags (“drag seals”) had FMRs elevated 22% above other short-trip seals (Fig. 3.2), operating at approximately 1.37 (± 0.05) Kleiber predictions of basal metabolism (Table 3.1). This was likely the result of increased locomotion costs, with drag seals flipper stroking consistently faster than normally-swimming short-trip seals (Fig. 3.4), potentially pushing up against a biomechanically constrained maximum rate. With more energy partitioned toward the fuelling of flipper strokes (16.7% versus 3.8%), drag seals were able to partition relatively little ingested energy toward growth (11.7% versus 32%) (Fig. 3.5), despite prey capture rates comparable with those of pregnant females (Fig. 3.6).

These results suggest that elephant seals fuel their substantial growth costs during their foraging migrations by engaging in stereotypic, energy-saving flipper stroking behaviors that keep locomotion costs low, and that increasing these costs can have substantial impacts on foraging success. This has implications for the ability of elephant seals to adapt to disturbance in important feeding grounds, with avoidance behaviors predicted to reduce time spent foraging while increasing time spent in transit – a disruption of routine swimming behaviors that inflates normally-low locomotion costs, thereby reducing energy available to the seal for partitioning towards growth. We predict that this effect would be exacerbated in pregnant, long-trip seals, which are potentially operating at or near a lower physiological limit to metabolism in order to adequately and rapidly build fuel reserves in support of an energetically costly lactation period.

### 3.4.5 Conclusions

By accounting for each of the costs associated with foraging, we can assess the efforts free-living animals spend acquiring resources, and thus, their overall energy requirements. Northern elephant seals have adopted a foraging strategy that utilizes an extreme energy economy, with FMRs that are (1) 75-85% lower than predicted for carnivores of their size (Nagy et al., 1999); (2) 45-65% lower than predicted for marine mammals of their size (Boyd, 2002); and (3) 41% lower than what has been measured in freely-diving Weddell seals of similar size, and for similar diving durations (eq. 3 in Williams et al. 2004a). Body mass was the most important determinant of FMR in our study, with a particularly dramatic effect of pregnancy such that, in the largest long-trip seals, Kleiber predictions of mammalian basal metabolism actually overestimated total at-sea energy expenditure. Pregnant seals were able to suppress their FMRs as body condition improved, thereby reducing the frequency of flipper strokes, and also by further reducing basal maintenance metabolism by an additional 21% compared to non-pregnant seals during the short trip. In contrast to normally-swimming seals, those instrumented with bulky, non-streamlined acoustic tags experienced elevated FMRs as a result of increased locomotion costs, significantly reducing foraging success and the net energy available for growth in these seals. Collectively, these results suggest that elephant seals keep overall energy requirements, and thus prey requirements, relatively low during their foraging migrations by engaging in adaptively stereotyped flipper stroking behaviors that minimize locomotion costs and, most likely, maintenance metabolism while diving. Minimization of these work costs frees up more of the energy ingested from prey items for fuelling of production, namely, accumulation of energy reserves for support of maintenance metabolism while fasting on land, and for pregnant seals, gestation and lactation.

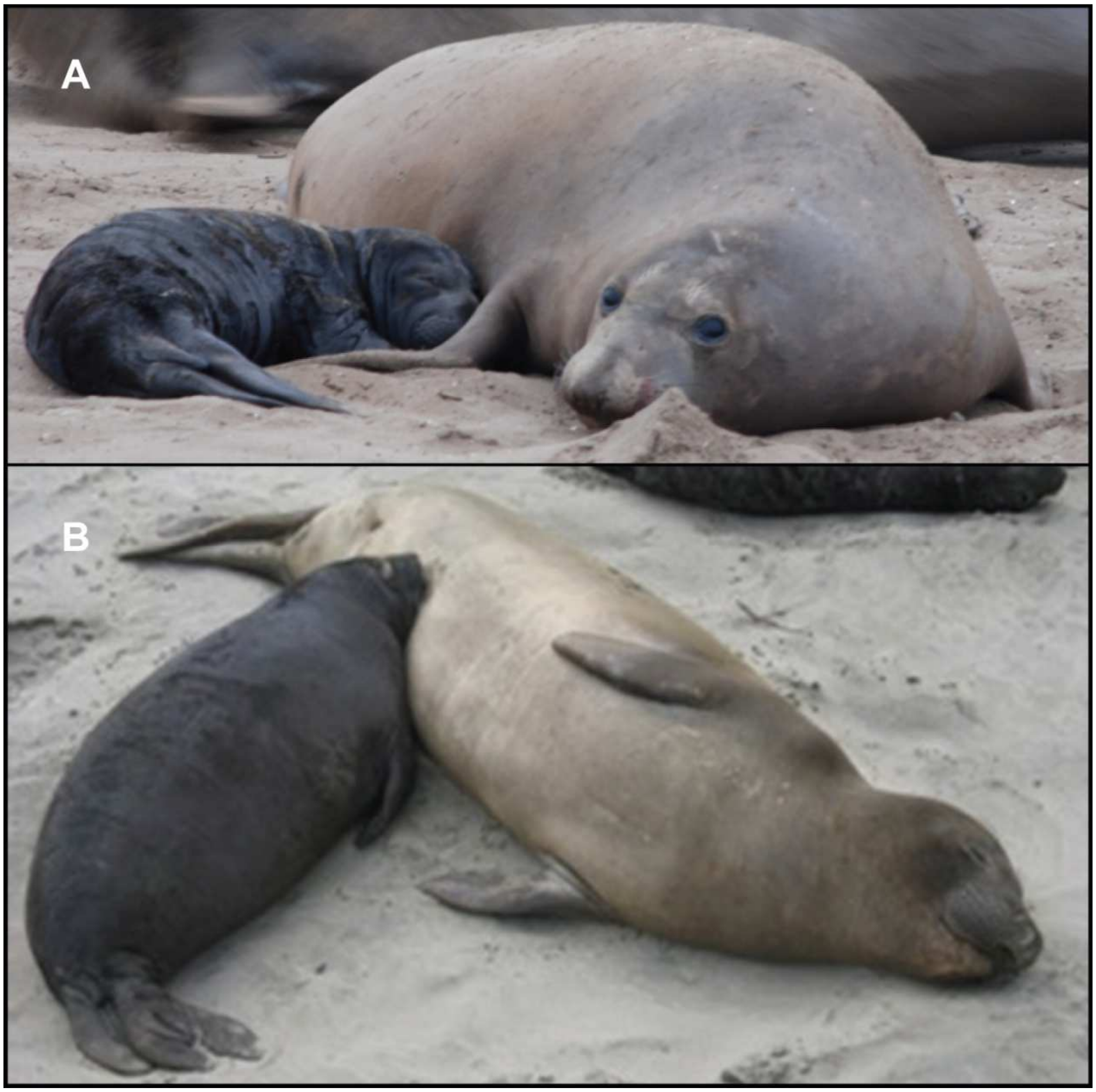


**Figure 3.1. Northern elephant seal mother with (A) young pup (1-2 d) and (B) pup just before weaning (25-28 d).** Photo credits: D. Costa, M. Fowler.

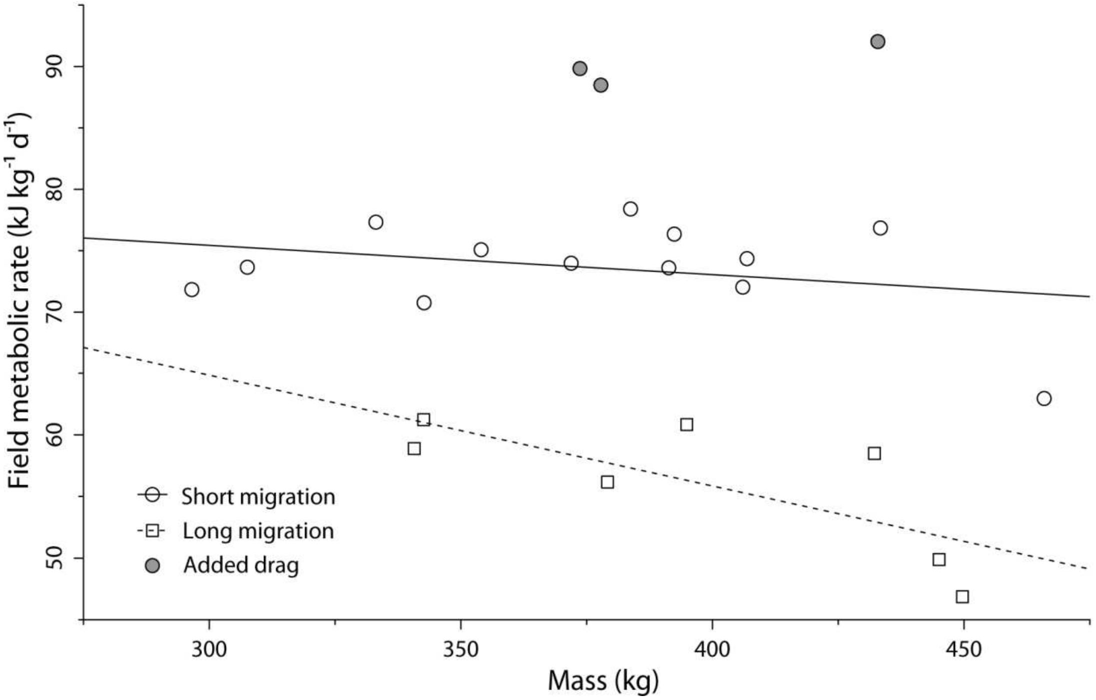


**Figure 3.2. Mass-specific field metabolic rates of northern elephant seals based on total number of flipper strokes executed during their foraging migrations, as a function of mass.** Filled circles indicate seals carrying added drag during their short migrations. See text for equations.

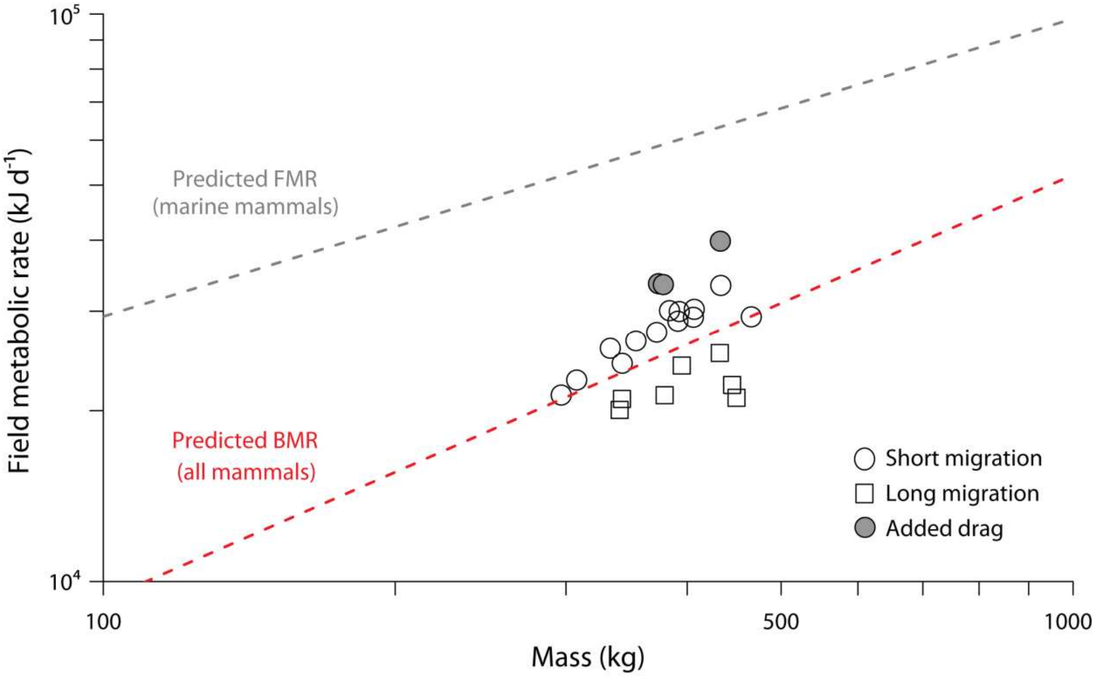


**Figure 3.3. Field metabolic rates of northern elephant seals compared to Kleiber (1975) predictions of mammalian basal metabolic rate (BMR) (dashed red line) and Boyd (2002) predictions of marine mammal field metabolic rate (FMR) (dashed grey line), as a function of mass.** Compared to seals during their short migration, seals of similar average body mass had 23% lower FMRs during the long migration according to the equation $FMR_{LT} = 19.5M + 14389$.

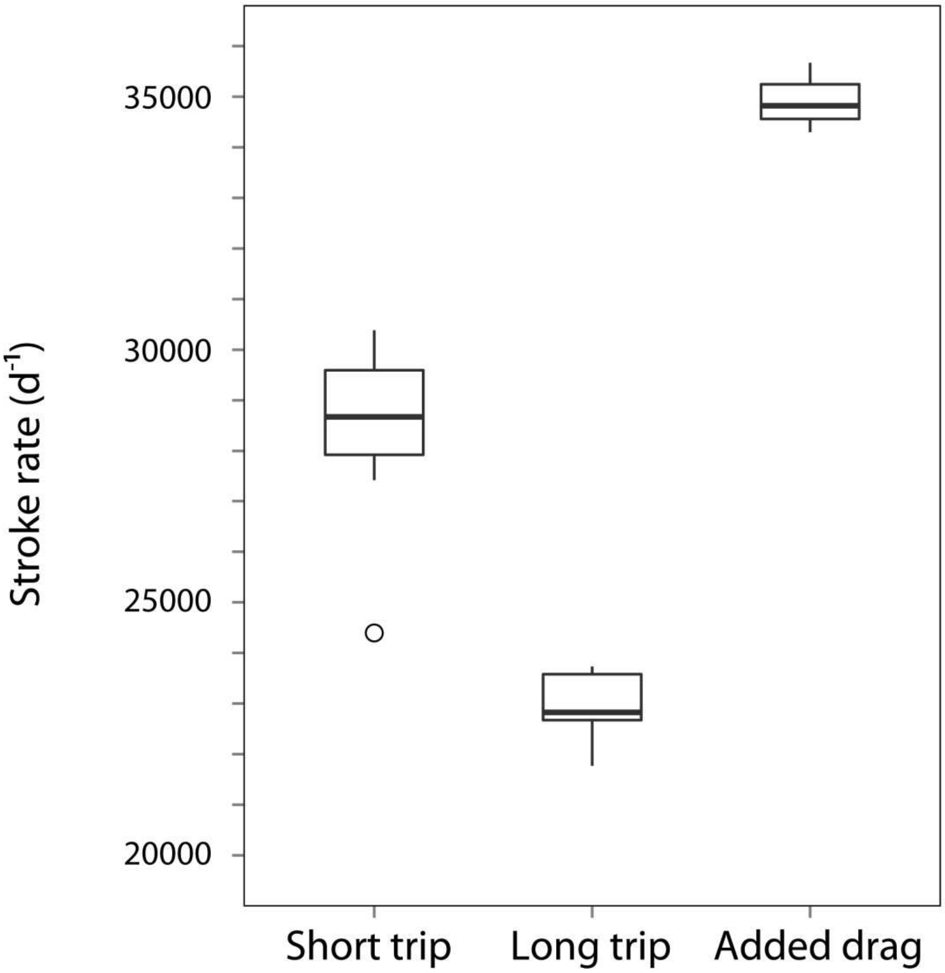


**Figure 3.4. Flipper stroke rates were higher for seals swimming normally during the short foraging trip (N = 13) than during the long foraging trip (N = 7).** In comparison, seals swimming with added drag during their short trips (N = 3) stroked consistently faster than normally-swimming seals during the same time (Welch two-sample t-test, $t = -9.7674$, $df = 7.471$, $p < 0.001$). Dark horizontal bars represent median (50th percentile) values while the lower and upper limits of the boxes represent the 25th and 75th percentiles, respectively. Whiskers correspond to the 1.5 interquartile range, and points represent outliers.

**Figure 3.5. Partitioning of ingested energy among work (grey tones) and production (warm tones) costs in foraging elephant seals.** Absolute costs for each seal are shown in the white panels (A), while proportions of total costs are averaged across the three groups in the grey panel (B), where ST = seals during the short foraging trip, LT = seals during the long foraging trip, and DG = seals with added drag during the short trip. Within each group, seals are listed from left to right in order of increasing body size. If locomotion costs on a per-stroke basis in LT seals are similar to those of ST seals, basal metabolism would have to be suppressed by approximately 21% in pregnant seals (see text).

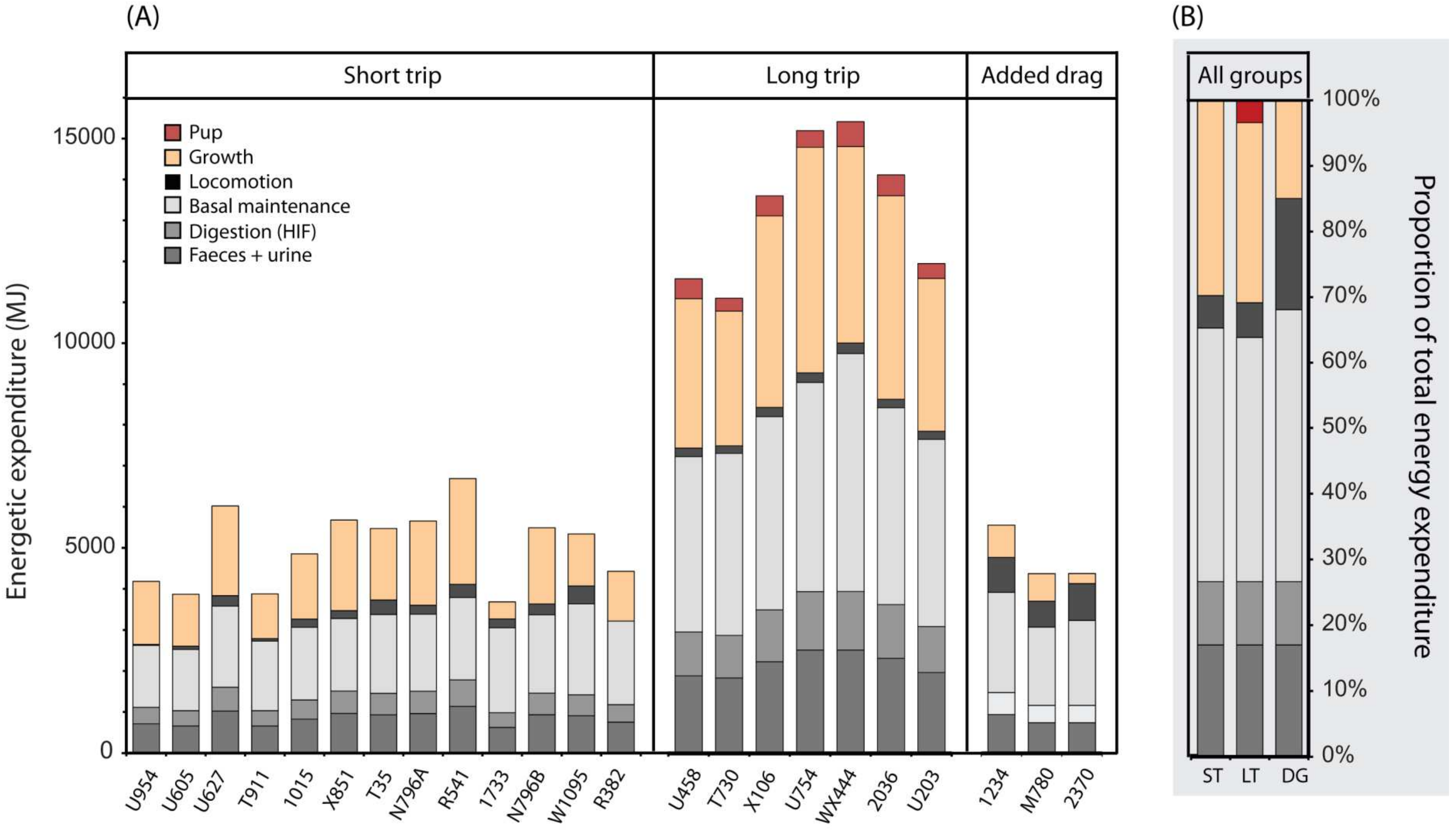
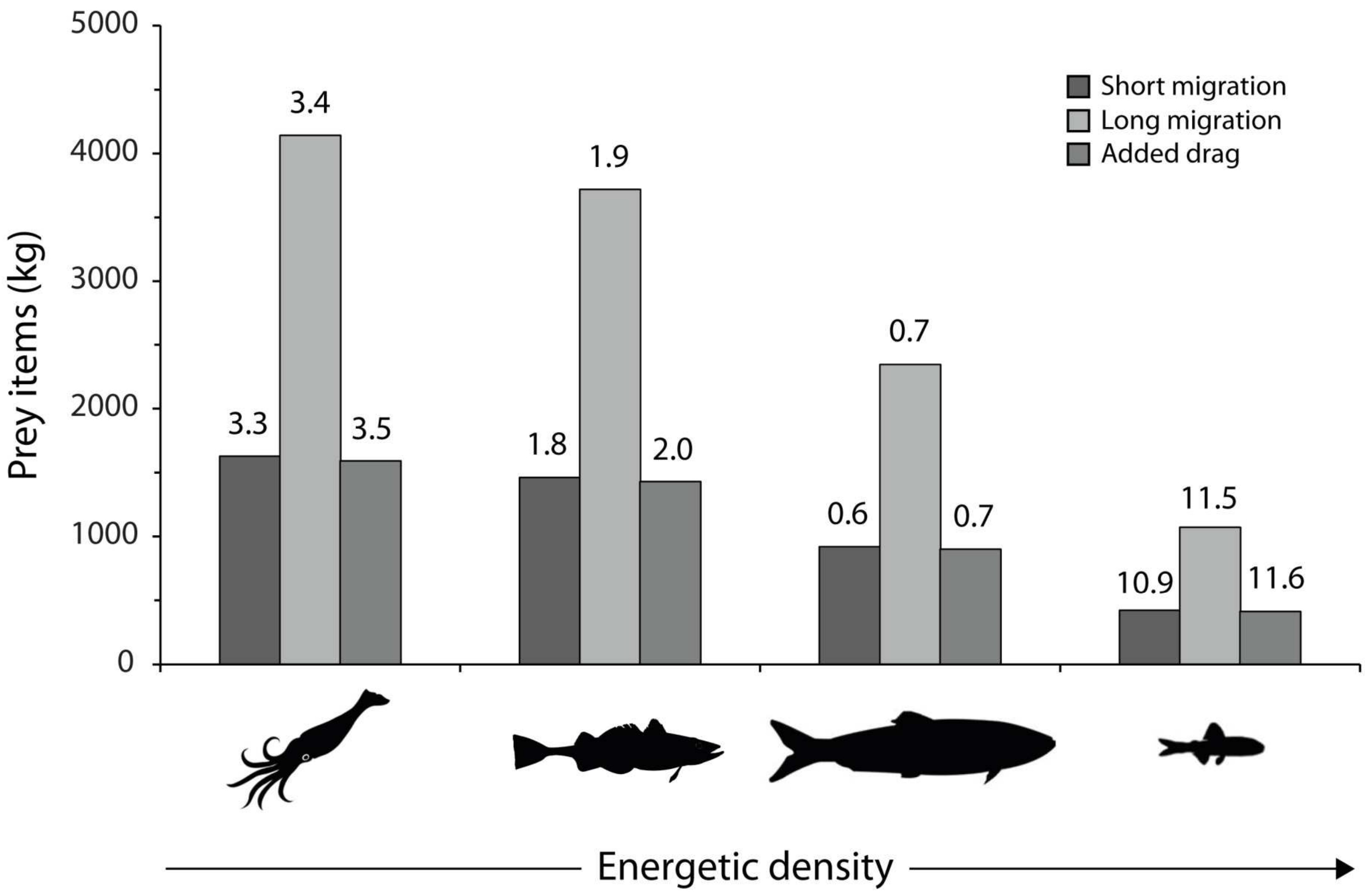

(A)
Short trip
Long trip
Added drag
Pup
Growth
Locomotion
Basal maintenance
Digestion (HIF)
Faeces + urine
Energetic expenditure (MJ)
15000
10000
5000
0
U954
U605
U627
T911
1015
X851
T35
N796A
R541
1733
N796B
W1095
R382
U458
T730
X106
U754
WX444
2036
U203
1234
M780
2370
(B)
All groups
100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
Proportion of total energy expenditure
ST
LT
DG

**Figure 3.6. Average prey requirements of adult female northern elephant seals across an entire foraging migration as a function of prey item's energetic density, assuming an average mass for each prey species.** From left to right, prey items include squid (*Octopoteuthis deletron*, 0.20 kg, 3.08 MJ $kg^{-1}$*),* Pacific hake (*Merluccius productus*, 0.32 kg, 3.43 MJ $kg^{-1}$), Pacific herring (*Clupea pallasii*, 0.55 kg, 5.44 MJ $kg^{-1}$) and lantern fish (F. myctophidae, 0.02 kg, 11.88 MJ $kg^{-1}$). Numbers above bars indicate the number of that particular prey item that would need to be captured per foraging dive in order to support at-sea energy expenditure, assuming a simple, monophagous diet. The diet of elephant seals, while unknown, likely includes a mix of these and other species of different sizes, and therefore true prey capture numbers and rates will vary from this idealized depiction. Sources: (Beamish and McFarlane, 1985; Clarke et al., 1985; Ohizumi et al., 2003; NOAA-OPR, 2008).


Prey items (kg)
5000
4000
3000
2000
1000
0
Short migration
Long migration
Added drag
3.3
3.4
3.5
1.8
1.9
2.0
0.6
0.7
0.7
10.9
11.5
11.6
Energetic density

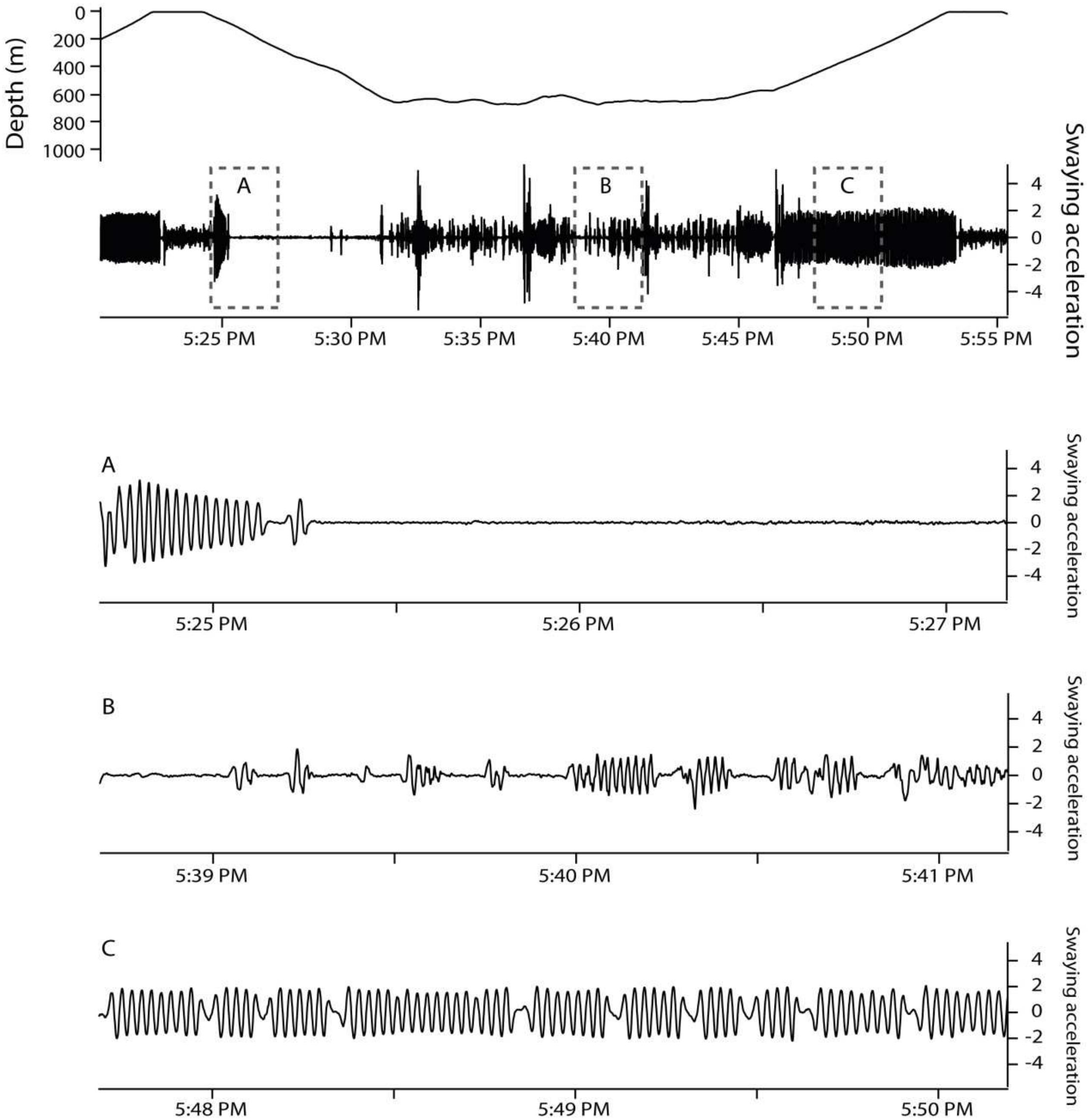


**Figure 3.7. Flipper stroking follows a predictable pattern along the course of each dive.** The top panel shows one foraging dive during the short migration of seal X851, where depth is shown with corresponding swaying acceleration. Grey boxes outline approximately 2.5-minute segments of flipper stroking, each representing one of the three main phases of a dive cycle: (A) descent, (B) foraging at depth, and (C) ascent. Note the consistent, high frequency flipper stroking occurring during ascent, when elephant seals are working against their negative buoyancy at depth in order to surface.

**Table 3.1. Summary of energy costs for all seals instrumented with accelerometers (N = 23).**

*Denotes LT (long foraging trip, pregnant) seals, N = 7; grey shading denotes DG (with added drag) seals, N = 3; all other seals are ST (short foraging trip) seals, N = 13.

"Avg Mass" is the seal's mass averaged across the entire migration, based on her weight at the beginning and end of the trip. "DAS" is the total number of days at sea recorded by the accelerometer (Acc) and time-depth recorder (TDR). Due to the high sampling frequency of accelerometers, it was common for the battery life of the instrument to expire before the seal had returned to shore. "Flipper Strokes" refers to the total number of flipper strokes recorded during the migration, and "FMR" refers to estimated field metabolic rates based on Flipper Strokes and a cost-per-stroke of 2.58 J $kg^{-1}$. "FMR (Kleiber)" is a multiplier of Kleiber (1975) predictions of mammalian basal metabolic rate. "Total E Spent" is the total amount of energy spent during foraging. See text for equations.

| **Seal** | **Avg Mass (kg)** | **DAS (Acc)** | **DAS (TDR)** | **Flipper Strokes** | **FMR (kJ kg$^{-1}$ d$^{-1}$)** | **Kleiber** | **Total E Spent (MJ)** |
|---|---|---|---|---|---|---|---|
| U954 | 297 | 71.7 | 71.9 | 1996414 | 71.8 | 1.02 | 1531 |
| U605 | 308 | 69.1 | 69.5 | 1973164 | 73.7 | 1.05 | 1574 |
| U627 | 333 | 86.6 | 86.6 | 2594365 | 77.3 | 1.13 | 2230 |
| T911 | 343 | 72.4 | 72.5 | 1986025 | 70.8 | 1.04 | 1758 |
| 1015 | 354 | 73.9 | 74.1 | 2149944 | 75.1 | 1.11 | 1970 |
| X851 | 372 | 71.2 | 71.2 | 2041792 | 74.0 | 1.11 | 1959 |
| T35 | 384 | 75.5 | 75.6 | 2295325 | 78.4 | 1.18 | 2273 |
| N796A | 391 | 70.0 | 72.8 | 1997358 | 73.6 | 1.12 | 2096 |
| R541 | 392 | 77.7 | 77.7 | 2300074 | 76.4 | 1.16 | 2329 |
| 1733 | 406 | 78.2 | 78.2 | 2184581 | 72.0 | 1.10 | 2287 |
| N796B | 407 | 65.3 | 71.8 | 1881764 | 74.4 | 1.14 | 2171 |
| W1095 | 433 | 60.5 | 79.5 | 1800692 | 76.8 | 1.20 | 2649 |
| R382 | 466 | 69.1 | 69.3 | 1685372 | 62.9 | 1.00 | 2033 |
| U458* | 341 | 147.6 | 222.1 | 3368761 | 58.9 | 0.86 | 4457 |
| T730* | 343 | 124.8 | 218.8 | 2962640 | 61.2 | 0.90 | 4591 |
| X106* | 379 | 147.8 | 230.8 | 3218611 | 56.2 | 0.85 | 4914 |
| U754* | 395 | 136.9 | 221.1 | 3228768 | 60.8 | 0.93 | 5311 |
| WX444* | 432 | 144.9 | 238.7 | 3284488 | 58.5 | 0.91 | 6035 |
| 2036* | 445 | 131.3 | 224.5 | 2538486 | 49.9 | 0.78 | 4984 |
| U203* | 450 | 129.9 | 224.5 | 2358871 | 46.9 | 0.74 | 4732 |
| 1234 | 374 | 100.6 | 100.8 | 3503199 | 89.8 | 1.35 | 3382 |
| M780 | 378 | 78.0 | 78.1 | 2676563 | 88.5 | 1.33 | 2611 |
| 2370 | 433 | 66.5 | 76.6 | 2371429 | 92.0 | 1.43 | 3051 |
| **Mean ST**<br>(s.d.) | **376**<br>(48.5) | | | | **73.6**<br>(3.9) | **1.10**<br>(0.06) | **2066**<br>(314) |
| **Mean LT**<br>(s.d.) | **398**<br>(46.1) | | | | **56.1**<br>(5.6) | **0.85**<br>(0.07) | **5003**<br>(534) |
| **Mean DG**<br>(s.d.) | **395**<br>(33.1) | | | | **90.1**<br>(1.8) | **1.37**<br>(0.05) | **3015**<br>(387) |

**Table 3.2. Summary of mass and energy gains for all seals instrumented with accelerometers (N = 23).**

*Denotes LT (long foraging trip, pregnant) seals, N = 7; grey shading denotes DG (with added drag) seals, N = 3; all other seals are ST (short foraging trip) seals, N = 13.

Mass Gain (%) is the increase in mass (post-migration) as a percentage of initial body mass (pre-migration). “Net E Gained” is the net energy gained during the foraging migration, and “Gross E Gained” is gross energy intake from prey before assimilation and digestion costs are deducted. See text for equations.

| Seal | Mass Gain (%) | Adipose Gain (kg) | Lean Gain (kg) | Net E Gain (MJ) | Gross E Gain (MJ) |
|---|---|---|---|---|---|
| U954 | 31.7 | 35.3 | 45.8 | 1539 | 4185 |
| U605 | 27.8 | 27.1 | 48.0 | 1266 | 3869 |
| U627 | 43.7 | 49.2 | 70.3 | 2187 | 6021 |
| T911 | 20.3 | 23.6 | 39.7 | 1086 | 3877 |
| 1015 | 21.9 | 39.4 | 30.6 | 1589 | 4851 |
| X851 | 31.1 | 54.1 | 45.9 | 2205 | 5676 |
| T35 | 25.2 | 41.2 | 44.9 | 1742 | 5472 |
| N796A | 29.5 | 48.6 | 52.0 | 2051 | 5652 |
| R541 | 37.2 | 61.9 | 61.1 | 2579 | 6688 |
| 1733 | 11.8 | 4.4 | 40.8 | 413 | 3681 |
| N796B | 26.9 | 42.8 | 53.7 | 1856 | 5488 |
| W1095 | 17.9 | 28.1 | 43.2 | 1268 | 5339 |
| R382 | 15.5 | 27.1 | 40.0 | 1215 | 4426 |
| U458* | 96.0 | 66.4 | 202.6 | 3635 | 11029 |
| T730* | 66.4 | 68.8 | 132.9 | 3280 | 10727 |
| X106* | 89.5 | 98.5 | 183.9 | 4655 | 13042 |
| U754* | 103.7 | 121.0 | 188.7 | 5480 | 14707 |
| WX444* | 78.4 | 97.9 | 205.5 | 4768 | 14723 |
| 2036* | 117.6 | 87.3 | 292.2 | 4944 | 13531 |
| U203* | 65.1 | 72.0 | 185.0 | 3721 | 11520 |
| 1234 | 11.8 | 18.8 | 22.9 | 810 | 5714 |
| M780 | 8.9 | 16.7 | 15.5 | 690 | 4499 |
| 2370 | 16.6 | -0.4 | 41.7 | 252 | 4501 |
| **Mean ST** | **26.2** | **37.1** | **47.4** | **1615** | **5017** |
| (s.d.) | (8.8) | (15.2) | (10.2) | (577) | (942) |
| **Mean LT** | **88.1** | **87.4** | **198.7** | **4355** | **12754** |
| (s.d.) | (19.5) | (19.9) | (47.7) | (811) | (1682) |
| **Mean DG** | **12.4** | **11.7** | **26.7** | **584** | **4905** |
| (s.d.) | (3.9) | (10.5) | (13.5) | (294) | (700) |

# Chapter 4

# One marine mammal is not like the other: sampling bias inflates perceptions of metabolic energy demand in aquatic carnivores

**JL Maresh, TM Williams, DP Costa**

## Abstract

In this review, we revisit and question the prevailing hypothesis that metabolism in marine mammals is different from, and more generalizable than, that of other mammals. We present evidence to show that the existence costs of marine species are highly variable and likely subject to the same influences as those of other mammals. We suggest that the axiomatic inertia behind the persistent perception of otherwise is an artifact of the methodological challenges inherent in obtaining empirical measurements from aquatic animals. For basal metabolism, these challenges mandate the collection of data that do not adhere to a set of methodological standards, rendering comparisons with terrestrial species inappropriate. For

measurements of field metabolism, the vast majority of marine mammal species are simply intractable. This leads to biases in study species, and the use of non-empirical estimates extrapolated from small-bodied, high-energy species for large-bodied species with zero empirical measurements. Synthesis studies thus tend towards oversimplification of what is in fact a complex issue for an entire group of mammals as different in their individual, metabolism-influencing traits as are terrestrial mammals. While some marine mammals may well have elevated existence costs, we will argue that this is not a shared characteristic of all 125+ species of marine mammals and that the increasing number of studies reporting low-to-moderate costs do not represent exceptions to the rule, but rather, legitimate indications of a different set of rules. We present evidence to support the hypothesis that marine mammals are comparable to other mammals in their energy needs, and that they are indeed indistinguishable from other carnivores in this regard. We suggest that, as is the case for all animals, existence costs for marine mammals are an emergent property of a collection of myriad behavioral and life history traits, rather than a simple and predictable product of the physics of their environment.

## 4.1 Marine mammal energetics

All biological activities depend on metabolic energy, and thus understanding why rates of metabolism vary is of fundamental importance.

A major factor affecting metabolic rate is body size – it is well-established that metabolic demand decreases on a mass-specific basis with increasing size in all animals (Brody and Procter, 1932; Benedict, 1938; Kleiber, 1975). For mammals, body size alone accounts for up to 96% of the variation in metabolic demand, with an additional 1% explained by infraclass membership such that marsupials generally have lower metabolic rates than their eutherian counterparts (Hayssen and Lacy, 1985; McNab, 1986b, 1988; Nagy, 1994, 2005). However, residual variation is still considerable at over six orders of magnitude among similarly-sized eutherians. Much of this residual variation can be explained by differences between animals in their ecology (e.g., diet and habitat) and phylogenetic history, as well as in simply the scale and timing of measurements (e.g., fluctuations due to circadian rhythms and seasonality) (Hayssen and Lacy, 1985; Müller, 1985; McNab, 1986a, 1988; Nagy, 1994; Nagy et al., 1999; Nagy, 2005; White et al., 2009; Hudson et al., 2013). However, up to two orders of magnitude in residual variation still remain even after accounting for these various factors (Nagy, 2005). The idea that any animal's energy demands are determined by a complex, collective suite of individual traits is thus well-supported and the statement "metabolism is complicated" is not a trivial one.

Specialization for aquatic living has occurred independently in three mammalian orders: the sirenians (manatees and dugongs), cetaceans (porpoises, dolphins and whales), and carnivores. Within the carnivores there were three separate transitions to a marine existence: pinnipeds (sea lions, fur seals, true seals and walruses), sea otters, and polar bears. As is the case for mammals on land, marine species cover a wide range of habitats, foraging techniques, morphological adaptations and reproductive strategies. Based on this diversity, we might expect different metabolic adaptations between the groups (Hunter et al., 2000; Worthy, 2001; Costa, 2009; Costa and Shaffer, 2012). However despite this, and despite mounting evidence to the contrary, there remains a pervasive, widely–accepted expectation in the scientific community that elevated metabolic rates are and should be a shared characteristic of all aquatic mammals (e.g., McNab, 1986a; Speakman and Krol, 2010; Hudson et al., 2013).

This perception took root when early studies on captive marine mammals reported remarkably low diving metabolic rates relative to higher-than-expected "resting" values (Irving et al., 1935; Scholander, 1940; Irving et al., 1941; Scholander et al., 1942), and gained further traction in subsequent decades as a substantial number of studies reported results similarly suggestive of high resting metabolisms (Irving and Hart, 1957; Hart and Irving, 1959; Hart and Fisher, 1964; Kanwisher and Sundnes, 1965; Ridgway and Patton, 1971; Sergeant, 1973; South et al., 1976; Scheffer, 1981; Kanwisher and Ridgway, 1983; Snyder, 1983). As early as the 1970s and 80s, however, several authors began challenging the validity of this generalization with measurements demonstrating otherwise, and/or by questioning the methodologies and comparability of early studies (Øritsland and Ronald, 1975; Gallivan and Ronald, 1979; Gaskin, 1982; Lavigne et al., 1986; Yasui and Gaskin, 1986; Worthy et al., 1987). For example, testing conditions during a large number of basal metabolic studies on marine mammals did not conform to the standard set considered necessary for comparability across species – the so-called Kleiber criteria (e.g., Irving et al., 1935; Scholander, 1940; Irving et al., 1941; Scholander et al., 1942; Irving and Hart, 1957; Hart and Irving, 1959; Kanwisher and Sundnes, 1965; Iversen and Krog, 1973; Wahrenbrock et al., 1974; Miller and Irving, 1975; Hampton and Whittow, 1976; Miller et al., 1976; South et al., 1976; Elsner et al., 1977; Heath et al., 1977; Blix et al., 1979; Craig Jr. and Påsche, 1980). Instead, test subjects were oftentimes young, growing animals, were not post-absorptive and/or were forcibly restrained and therefore very likely stressed – all conditions known to elevate metabolism (Kleiber, 1975). As a result, marine mammals appeared to have resting metabolisms twice as high as terrestrial mammals.

Recent review studies have argued that when metabolism determinations not satisfying Kleiber's criteria for basal conditions are removed from analyses, marine mammals do not differ from terrestrial mammals measured under similar conditions (Lavigne et al., 1986; Hunter et al., 2000). While these studies were compelling, they did not succeed in overturning what was and continues to be a surprisingly tenacious perception of marine mammals as especially voracious consumers. The issue is far from settled, however, and there is currently much discussion on the topic, with no resolution. Much of the disagreement no doubt stems from the lack of consensus over what exactly qualifies as "basal" conditions for aquatic animals (Williams et al., 2001; Boyd, 2002; Costa, 2009). For example, all measurements of basal metabolism in terrestrial animals take place in air, but it is unclear whether this is always appropriate for aquatic animals. On the one hand, measurements taken in air, while appealingly comparable to studies on terrestrial mammals, might be somewhat meaningless as many marine mammals spend most-to-all of their lives submerged to some degree. On the other hand, as endotherms, marine mammals are theoretically less likely to meet the Kleiber requirement of thermal neutrality if measured in water, where elevated metabolisms should be necessary to offset high rates of heat loss (Hart and Fisher, 1964; South et al., 1976; Dejours, 1987; Speakman and Krol, 2010; Hudson et al., 2013). And then there are some who believe that where the measurement occurs makes no difference (Irving and Hart, 1957; Lavigne et al., 1986).

Interestingly, some recent studies show that, contrary to what would be predicted based on thermoregulation arguments, metabolic rates of quiescent marine mammals after prolonged submergence are actually indistinguishable from the basal metabolic rates expected for similarly-sized terrestrial mammals (Hurley and Costa, 2001; Williams et al., 2004a). These results suggest that measurements from aquatic animals resting on land might be inflated, providing support for the viewpoint that measurements taken in water might be more representative of truly basal conditions for aquatic animals. However, physiological adjustments associated with the dive response would be expected to reduce the metabolic rate of any submerged animal, and particularly so for marine mammals. In addition, marine mammals differ in their degree of amphibiousness, which seems to be correlated with energy expenditure such that animals subject to repeated breath-holds are able to suppress their metabolisms as a tissue-level defense against chronic hypoxia (Hassrick et al., 2010; Vazquez-Medina et al., 2011; Tift et al., 2013). Collectively, these physiological complications of an aquatic existence further challenge a consensus on a universal set of measurement conditions for all marine mammals. Many studies thus avoid the use of the "basal" label and instead report baseline measurements as "standard" or "resting" metabolic rates, in acknowledgement of lack of strict conformity to Kleiber's criteria developed for terrestrial mammals (e.g., Hurley and Costa, 2001; Sparling et al., 2006; Williams et al., 2011).

In light of the confusion surrounding measurements of basal metabolism in marine mammals, perhaps a better approach to understanding their energy needs relative to terrestrial mammals is to also consider daily energy needs, or field metabolic demand. Basal metabolism, or so-called metabolic overhead, represents the minimum energy required for the survival of a sedentary, alert-but-calm, thermally-neutral, non-growing animal unconcerned with feeding or reproduction (Kleiber, 1975). This is very rarely the situation for most organisms. Field metabolism, in contrast, captures the sum costs of metabolic overhead and all daily activities. Field metabolism is arguably, then, the more ecologically relevant measurement of comparison between species, as it represents the energy required to fuel all of the complex behaviors associated with "real life." Indeed, field metabolic rate is likely to be the more relevant measure for managers interested in understanding the prey requirements of high-level predators such as marine mammals.

Similar to the prevailing theory on basal costs, field costs are generally believed to run high in marine mammals. This conclusion is based in large part on what we argue are two major issues with models attempting to construct a unifying set of predictions of energy needs for marine mammals: (1) sampling bias towards smaller, more active species and (2) inclusion of non-empirical estimates for large-bodied species, which are themselves extrapolated using allometric scaling relationships derived from (1).

### 4.1.1 Sampling bias

Synthesis studies concluding high existence costs in marine mammals tend to rely mostly on a small number of measurements from sea otters (Yeates et al., 2007) and otariids seals (sea lions and fur seals) (Costa et al., 1985; Costa and Gentry, 1986; Costa et al., 1989; Costa et al., 1991; Arnould et al., 1996; Costa and Gales, 2003) *in situ*, and a few small odontocete species (dolphins and porpoises) in captivity (Kreite, 1995; Kastelein et al., 2002). These groups share the critical characteristic of being relatively tractable study species compared to the other, mostly unstudied groups, and for the most part, both "basal" and field metabolism run consistently high in these animals. This is not surprising as large energy requirements in otters, otariids and small odontocetes would be consistent with their highly active lifestyles and high-energy swim behaviors (Crocker et al., 1994; Fish, 1994). Sirenians (manatees and dugongs) and some phocid seals (true seals), however, represent notable and numerous empirical exceptions to elevated metabolisms in marine mammals (e.g., Gallivan and Best, 1980; Kooyman et al., 1980; Irvine, 1983; Ronald et al., 1984; Davis et al., 1985; Sakamoto et al., 1989; Markussen et al., 1990; Bowen et al., 1992; Castellini et al., 1992; Ponganis et al., 1993; Hedd et al., 1997; Williams et al., 2011; Maresh et al., 2014). In contrast to the other commonly measured groups described above, sirenians and phocid seals have low metabolic rates suggestive of an energy economy strategy that is consistent with the more moderate activity levels observable in these groups (Crocker et al., 1994; Fish, 1994; Kojeszewski and Fish, 2007; Costa, 2009). In analytical models, a logical consequence of overrepresentation of smaller species with more active lifestyles would be an inflated estimation of average costs and an overestimation of the metabolic energy demand of many of the less studied, larger-bodied, more energetically conservative species.

### 4.1.2 Extrapolated estimates

Despite the considerable number of studies reporting low-to-moderate existence costs in some marine mammals, they are considered exceptions to the general "rule" of high costs for all marine mammals. This rule is then applied in estimates of energy requirements of empirically inaccessible species such as baleen whales and the larger odontocete species. However, the assumption of large energy requirements in large-bodied marine mammals is not supported by the biology of the animals, particularly in baleen whales (mysticetes). First, mysticetes tend to resemble phocid seals in many key aspects of their behavior and life history, including the preference for economical swim speeds and behaviors (Crocker et al., 1994; Blix and Folkow, 1995; Woodward et al., 2006; Costa, 2009), adoption of a capital breeding strategy that includes extensive periods of fasting, and the undertaking of long distance migrations covering thousands of kilometers between feeding and breeding habitats (Costa, 1993; Costa and Shaffer, 2012). Second, mysticetes are predicted to have reduced existence costs by sheer virtue of their size, as swimming efficiency should increase, and rates of heat loss to the environment should decrease, in larger aquatic animals (Ryg et al., 1993; Watts et al., 1993; Boyd, 2002). Third, many mysticetes inhabit temperate or tropical waters at least seasonally if not year-round, and existence costs have been shown to be reduced in otariids living in warmer climates (Costa and Trillmich, 1988; Trillmich and Kooyman, 2001). Collectively these characteristics are suggestive of low existence costs in at least some baleen whales, making extrapolations from a handful of smaller-bodied, high-energy odontocetes inappropriate for this group.

## 4.2 The case for carnivory: are marine mammals really that different?

Even were the elevated metabolism generalization to hold true, some have noted that the high existence costs of many marine mammals measured to date are completely in line with those of other carnivores, that is approximately 1.4 – 2 times higher than those of herbivores and omnivores (hereafter referred to as “non-carnivores”) (Nagy, 1994) (but see Williams et al., 2001). The mechanism driving elevated metabolic rates in terrestrial carnivores is unclear, but hypotheses include high metabolic costs associated with consumption of a high protein diet (Lavigne et al., 1986), high metabolic demand of organs in the gastrointestinal tract (Ewer, 1973; Williams et al., 2001), the relatively high digestibility and nutritional payoff of vertebrate prey (McNab, 1986a; Shipman and Walker, 1989), and high-energy pursuit behaviors associated with prey capture (McNab, 1986a; Carbone et al., 2007). Whatever the reason(s), however, high existence costs are strongly correlated with carnivory in terrestrial mammals.

Carnivory is the rule for almost all marine mammals; manatees and dugongs (sirenians) are the only exception. While field metabolic demands are currently unmeasured in sirenians, their basal metabolic rates are as much as 85% below those predicted for eutherian mammals (Gallivan and Best, 1980; Irvine, 1983), suggesting that diet plays an influential role in dictating metabolic energy demand in the marine environment – and indeed, in *any* environment. If, as is the case for terrestrial mammals, elevated metabolisms in pinnipeds and cetaceans are driven by carnivory, this calls into question the thermoregulation argument oftentimes invoked to justify the assumption of elevated metabolisms in intractable species. It is assumed that, as endotherms, high metabolisms would be necessary to offset high rates of heat loss in an aquatic environment (e.g., Hart and Fisher, 1964; South et al., 1976; Dejours, 1987; Speakman and Krol, 2010; Hudson et al., 2013). Due to a high surface area to volume ratio, this is certainly the case for the smallest marine mammals, namely sea otters (*Enhydra lutris*) (Costa and Kooyman, 1984), very young otariid seals (Liwanag et al., 2009; Liwanag, 2010), and perhaps small porpoises (Watts et al., 1993). However, heat loss is predicted to be inconsequential for anything but the smallest aquatic mammals (Porter & Kearney 2009). Indeed, Boyd (2002) invoked first principles of hydrodynamics and thermoregulation to argue that *field* metabolic demands should converge on predicted *basal* metabolic demands in the very largest species. This has been demonstrated in 400-kg wild northern elephant seals (*Mirounga angustirostris*) (Maresh et al., 2014), indicating that heat loss is not an issue for large-bodied aquatic mammals.

If marine mammals resemble other carnivores in their energy needs, the most parsimonious hypothesis explaining elevated metabolisms in these high-level aquatic predators is that they are a byproduct of a carnivorous lifestyle, rather than that they are necessary to offset a theoretically high rate of heat loss. To test the carnivory hypothesis, we compared published basal/standard/resting metabolic rates (BMRs) and field metabolic rates (FMRs) between marine mammals and all other eutherian mammals, and between marine mammals and all other carnivores. For BMRs, comparisons were made both with and without data points for marine mammals measured under non-Kleiber conditions. For the latter, most discarded measurements were from juveniles and pups (pinnipeds) or were non-empirical estimates (killer whales and mysticetes). For FMRs, comparisons were made both with and without empirical measurements on wild animals. For the latter, most discarded measurements were from animals in captivity (pinnipeds) or were non-empirical estimates (mysticetes). A complete description of statistical analyses and data selection criteria can be found at the end of this chapter. Databases of BMR and FMR determinations used in this study can be found in Appendices A.1.1 and A.2.1, respectively. Given the dearth of empirical data on cetaceans, we are mostly limited to comparisons between pinniped species; however, we posit that many of the conclusions drawn from these comparisons apply to both groups for reasons discussed above.

### 4.2.1 "Basal" metabolic demand

When all measurements, regardless of measurement conditions, were included in analyses, marine mammals appeared to have significantly elevated BMRs compared to other eutherians (Fig. 4.1A). From these relationships, a 200-kg marine mammal would be predicted to have basal energy requirements approximately 2.5 times those of a 200-kg terrestrial mammal. When only animals measured under Kleiber conditions were compared (Fig. 4.1C), this same marine mammal would be predicted to have basal energy requirements approximately 1.8 times those of a terrestrial mammal.

When only carnivores were compared, differences between groups were further reduced: a 200-kg marine mammal is predicted to have 2.2 and 1.6 times the basal energy requirements of a similarly-sized terrestrial carnivore when all measurements, and only measurements meeting Kleiber standards are included, respectively (Figs. 4.1B, 4.1D). When comparing carnivores measured under Kleiber conditions, there were no significant differences between the slopes (ANCOVA, $F_{1,105} = 0.102$, $p = 0.75$) of the regression lines describing the relationship between BMR and mass for terrestrial carnivores and marine mammals, however, intercepts were significantly different (ANCOVA, $F_{1,106} = 16.68$, $p < 0.0001$).

With an updated dataset, our results were different from those of Lavigne et al. (1986) and Hunter et al. (2000) as we found basal/resting/standard metabolic rates of marine mammals to be significantly elevated above the basal metabolic rates of terrestrial mammals, even when comparisons included only Kleiber determinations and only carnivores. However, we argue that the confusion and lack of consensus surrounding measurements of basal metabolism in marine mammals should be considered a serious preclusion to interpretations of this kind of data. For example, our own analyses included many data points from individuals measured in air, rather than in water (when this information was even provided). No doubt these measurement decisions were based somewhat on the understanding that metabolic rate decreases during submergence, which would potentially confound the effort to isolate the effects of inactivity on metabolism. But it could be argued that in trying to separate a resting response from the dive response by measuring aquatic animals in air, data may be artificially inflated for animals who spend most of their lives submerged – for them, the aquatic physiology of resting during submergence might be the more relevant measure of truly basal conditions. Because the standards for measuring basal metabolism were created under conditions appropriate for animals on land, we caution against broad conclusions about the basal needs of marine mammals in comparative studies and suggest the use of FMR instead.

### 4.2.1 Field metabolic demand

When all measurements including those obtained on captive animals and including non-empirical estimates were included in analyses, the FMRs of marine mammals tended to be higher than those of similarly-sized eutherian mammals (Fig. 4.2A). From these relationships, a 200-kg marine mammal would be predicted to have a field metabolic rate approximately 1.4 times that of a 200-kg terrestrial mammal. This effect, however, was not significant (ANCOVA for slopes, $F_{1,122} = 1.577$, $p = 0.21$; ANCOVA for intercepts, $F_{1,123} = 3.244$, $p = 0.07$). When data were culled to include only empirical measurements on wild animals, differences were further reduced such that this same marine mammal would be predicted to have a field metabolic rate only 1.16 times that of a terrestrial mammal (Fig. 4.2C).

Similarities were stronger when only carnivores were compared (Fig. 4.2B). When all measurements were included, the predicted field metabolic rate of a 200-kg marine mammal was only 1.17 times that of a similarly-sized terrestrial carnivore. When data were culled to only include empirical measurements on wild marine carnivores, the predicted field metabolic rate of a 200-kg marine mammal was 0.98 times that of a similarly-sized terrestrial carnivore (Fig. 4.2D). Interestingly, the intercepts were not different between groups (ANCOVA, $F_{1,40} = 2.35$, $p = 0.13$), but the slope for marine mammals was significantly shallower that that for terrestrial mammals (ANCOVA, $F_{1,39} = 5.197$, $p = 0.03$), indicating that the field metabolic rates of larger marine mammals would actually be predicted to be less than that of a similarly-sized, large terrestrial carnivore (at body sizes over approximately 180 kg, red line in Fig. 4.2D). A shallower slope for marine mammals is in agreement with Boyd's (2002) predictions of the convergence of FMR and BMR at very large body sizes. But these results suggest that, for marine mammals measured to-date, field metabolic costs are not significantly higher than those of other mammals, and are indistinguishable from what would be predicted for other carnivorous mammals. Because of the significantly different slopes, however, we present the following equation to predict FMR in marine mammals:

$$\mathrm{FMR}_{\mathrm{MM}} = 732\ \mathrm{kg}^{0.49} \tag{4.1}$$

where $\mathrm{FMR}_{\mathrm{MM}}$ is the predicted field metabolic rate of a marine mammal in kcal $d^{-1}$ and kg is the animal's mass in kg ($r^2 = 0.43$, $F_{1,23} = 19.27$, $p < 0.001$). However, we caution against using this equation for anything other than a very coarse estimate of energy needs in a particular species, as actual field metabolic rates can vary substantially from predicted (see below).

## 4.3 Predicting metabolic energy demand for the average marine mammal

We were not able to find support for the hypothesis that marine mammals have elevated field metabolic demands compared to other mammals when data were culled to include only empirical measurements on wild animals. Instead we find support for the hypothesis that marine mammals have slightly elevated energy requirements compared to other mammals, but similar to those of other carnivores. These results suggest that the elevated field metabolic rate of the statistically average marine mammal is driven by diet, and that it does not differ from other carnivores in this regard. Given the confusion surrounding measurements and interpretations of BMR in marine mammals, as well as the more ecologically relevant measurement that FMR represents, we believe that these results demonstrate the importance of using FMR instead of BMR when comparing the metabolic energy demand and, by extension, prey resource requirements, of marine mammals.

## 4.4 Predicting metabolic energy demand for the individual marine mammal

It is clear from the information presented in Fig. 4.2D that while the average marine mammal may resemble the average terrestrial carnivore in terms of its existence costs, the variation around that average is considerable. It is also clear that each of the major marine groups represented empirically (sea otters, otariid seals, and phocid seals) tend to differ predictably in their relation to average predictions. Here we highlight differences between otariid and phocid seals, two groups that resemble each other morphologically but not consistently otherwise. Measured FMRs of phocid seals ranged from between 0.41–0.93 predicted for marine mammals (conditional mean of Y from eq. 4.1, this study), indicating that energy requirements will tend to be overestimated in this group. In contrast, measured FMRs of otariid seals ranged from between 0.89–2.06 predicted for marine mammals, indicating that energy requirements will tend to be underestimated. To put this into perspective, the predicted daily energy needs of a 200-kg marine mammal based solely on body size (eq. 4.1) would be approximately 9,900 kcal, yet a phocid seal's energy requirements would actually range from approximately 4,000 – 9,200 (average = 6,820) kcal while those of an otariid would range from 8,800 – 20,400 (average = 13,000) (Fig. 4.3, middle columns). When measurements from captive animals and non-empirical estimates on large-bodied animals are included in the predictive model as is traditionally the case (Fig. 4.2A, 4.2B), daily prey requirements for phocid seals are more severely overestimated at approximately 12,000 kcal (Fig. 4.3, left columns).

In either case, data do not support a general model for estimating food consumption rates of individual pinniped species. Instead, our analyses indicate that phocid seals, in general, have half the metabolic energy demand, and therefore half the prey requirements, of otariid seals. Similarities between the two major groups of pinnipeds may therefore be superficial, and it is probably not appropriate to equate one with the other in terms of energetics, especially as their actual energy needs encompass a very different set of predictions and conclusions about a consumer population's impacts on its prey resources. These results suggest that older models including all data regardless of how they were collected, are not only rife with uncertainty but also tend to inflate the average. Therefore, for other than the coarsest of estimates, more economical groups should be considered separately from high-energy groups.

No empirical measurements of FMR have been published for adult cetaceans in the wild. We hypothesize that odontocetes will tend to resemble otariid seals in their high metabolic energy demand, and mysticetes will tend to resemble phocid seals in their relative energy economy. For mysticete whales, we hypothesize that this effect would be exaggerated in the largest species, such as blue and fin whales (*Balaenoptera musculus*), while smaller species such as minke whales (*Balaenoptera acutorostrata*) might have existence costs closer to predicted values. In addition, we hypothesize that feeding technique would modulate this relationship between size and energy economy such that species with slower chase speeds (e.g., gray and right whales, *Eschrichtius robustus* and *Eubalaena spp.*) might have lower existence costs than species requiring faster chase speeds (e.g., humpback whales, *Megaptera novaeangliae*) (Woodward et al., 2006).

## 4.5 Conclusions

Understanding the metabolic energy demands of marine mammals is of interest to many groups: physiologists are interested in understanding how mammals have adapted to an aquatic existence; ecologists are interested in understanding the role these large predators play in their ecosystems; and managers are interested in understanding the impacts these consumers have on commercially valuable fish stocks. In contrast to the situation for many terrestrial animals, however, the difficulties inherent in obtaining empirical measurements of metabolic rate in far-ranging, large-bodied marine animals range from considerable to insurmountable. That any data exist in this regard is a testament to the creativity and resolve of the biologists determined to bring an important and interesting group of organisms into the collective understanding of how animals work. Yet for all of their merit, a careful approach in their application to comparative studies is warranted, especially as new data on a broader range of species become available. Sampling biases, inclusion of non-empirical estimates, and confusion over methodological standards render broad conclusions of exceptionally high metabolic energy demands in all marine species questionable.

For field metabolic rate, overrepresentation of smaller, more active species has the potential to inflate the average, misrepresenting the situation for groups with few-to-zero empirical measurements. In addition, scaling up measurements for some of the larger, least tractable species also introduces potential for error, especially in light of the considerable variation in metabolic energy demand between species that might resemble each other only superficially. This concept is demonstrated by the order of magnitude difference in measured field metabolic rates between similarly-sized pinnipeds (Fig. 4.3). Just as applying an otariid physiology to a phocid seal is potentially seriously problematic, applying odontocete metabolism to a mysticete whale is likewise probably inappropriate. Indeed, the relatively few data points available for large cetaceans will have a large influence on the overall relationship and these are some of the least confident measurements – they rely on estimates drawn from animals in captivity (odontocetes), from observations of prey ingestion rates of animals of unknown mass (mysticetes), or from smaller species using allometric scaling principles (odontocetes and mysticetes). Much of the false perception of marine mammals as generalizably high in their energy demands is no doubt a result of the lack of empirical metabolic data from these larger, slower-paced species.

Our results indicate substantial inter-species variation in metabolic energy demand that is not consistent with a view of marine mammals as one uniform “group” of species with universally high prey-energy requirements. The expectation that phocids, otariids, mustelids, odontocetes and mysticetes should employ the same metabolic response to their diverse ecologies and evolutionary histories is not supported by the data. Rather, field metabolic rates of marine mammals measured to-date are on average, and in their variability, comparable to those of other eutherian mammals, and indistinguishable from those of terrestrial carnivores. Much of the residual variation in marine mammal metabolism is likely influenced by the same drivers of metabolic demand as in terrestrial groups, namely, diet, habitat, phylogeny, and other environmental factors.

## 4.6 Datasets & methods

Basal metabolic rates (BMRs) determined for 565 eutherian mammals (N = 745 determinations) were obtained from three major sources: (1) data on terrestrial mammals synthesized in review papers by McNab (1986a) and White and Seymour (2003); (2) data on marine mammals compiled by Lavigne et al.’s (1986) review paper; and (3) data from individual studies of terrestrial mammals published since 2003 and of marine mammals since 1986. Every effort was made to verify data from the review papers with the original source (N = 264 of 273 original sources). Measurements were subsequently scored according to conformation to Kleiber criteria of basal metabolism, that is, whether the animal was an adult, in a post-absorptive state, was measured under thermally-neutral conditions, and was resting but alert (Kleiber, 1975). Measurements taken on restrained, sleeping or sedated animals were considered to be in violation of the resting requirement. In cases where conformation to Kleiber criteria was unclear, data points were discarded. BMRs were then compared between marine mammals and all other eutherian mammals, and between marine mammals and all other carnivores. These comparisons were made both with and without data points for marine mammals measured under non-Kleiber conditions. Sirenians, as the only herbivorous marine mammals, were removed from analyses with carnivores. The complete database of BMR determinations used in this study can be found in Appendix A.1.1.

Field metabolic rates (FMRs) determined for 106 eutherian mammals (N = 126 determinations) were obtained from three major sources: (1) data on terrestrial mammals synthesized in review papers by Nagy et al. (1999) and Carbone et al. (2007); (2) data on marine mammals compiled by Boyd (2002); and (3) data from individual studies of terrestrial mammals published since 2007 and of marine mammals since 2002. Every effort was made to verify data from the review papers with the original source (N = 94 of 99 original sources), and, unless otherwise noted, only data published for wild adult animals were used in the present study. FMRs were then compared between marine mammals and all other eutherian mammals, and between marine mammals and all other carnivores. Sirenians, as the only herbivorous marine mammals, were removed from analyses with carnivores. The complete database of FMR determinations used in this study can be found in Appendix A.2.1.

Note that, while most closely related to artiodactyls, we felt it appropriate to compare cetaceans with members of the order Carnivora (including pinnipeds and terrestrial carnivores) due to their exclusively carnivorous diet. We acknowledge, however, that some of the large whales feeding on krill might be more comparable to terrestrial invertebrate eaters outside Carnivora.

As is traditionally the case in allometric metabolism studies, simple least-squares linear regression models of log-transformed data were used in analyses, but relationships on untransformed data were expressed using the power function $y = ax^b$, where y is metabolic rate in kcal $day^{-1}$, x is the mass of the animal in kg, a is the mass coefficient, and b is the scaling exponent. When data are log-transformed, b and log(a) represent the slope and y-intercept of the linear regression, respectively. ANCOVAs were used to test for differences between the slopes and intercepts of allometric regressions. Confidence intervals (CIs) represent uncertainty in our estimate of the conditional mean $E(Y \mid X = x)$ due to sampling error. Prediction intervals (PIs) represent uncertainty in predicting individual responses and take into account variability in the conditional distribution $Y \mid X = x$. 95% CIs and PIs were calculated using the ‘predict’ function of the ‘lm’ package in R 2.15.3 (R Development Core Team, 2013).

**Figure 4.1. Basal metabolic demands of mammals when data for marine mammals include determinations made while not meeting Kleiber standards (top row), and when data include only determinations made while meeting Kleiber standards (bottom row).** The left column (A, C) shows comparisons among all eutherian mammals with regression lines bounded by 95% confidence intervals (grey shading bordered by dashed lines) and 95% prediction intervals (outer set of dashed lines) for terrestrial eutherians ($y = 59.2x^{0.70}$). The right column (B, D) shows comparisons among terrestrial carnivores and marine mammals with regression lines, 95% C.I. and 95% P.I. for terrestrial carnivores ($y = 70.9x^{0.70}$). Note that, for display purposes, grams are the units of mass in the figures while the equations are for units of mass in kilograms as described in the text. Each data point represents an individual measurement.

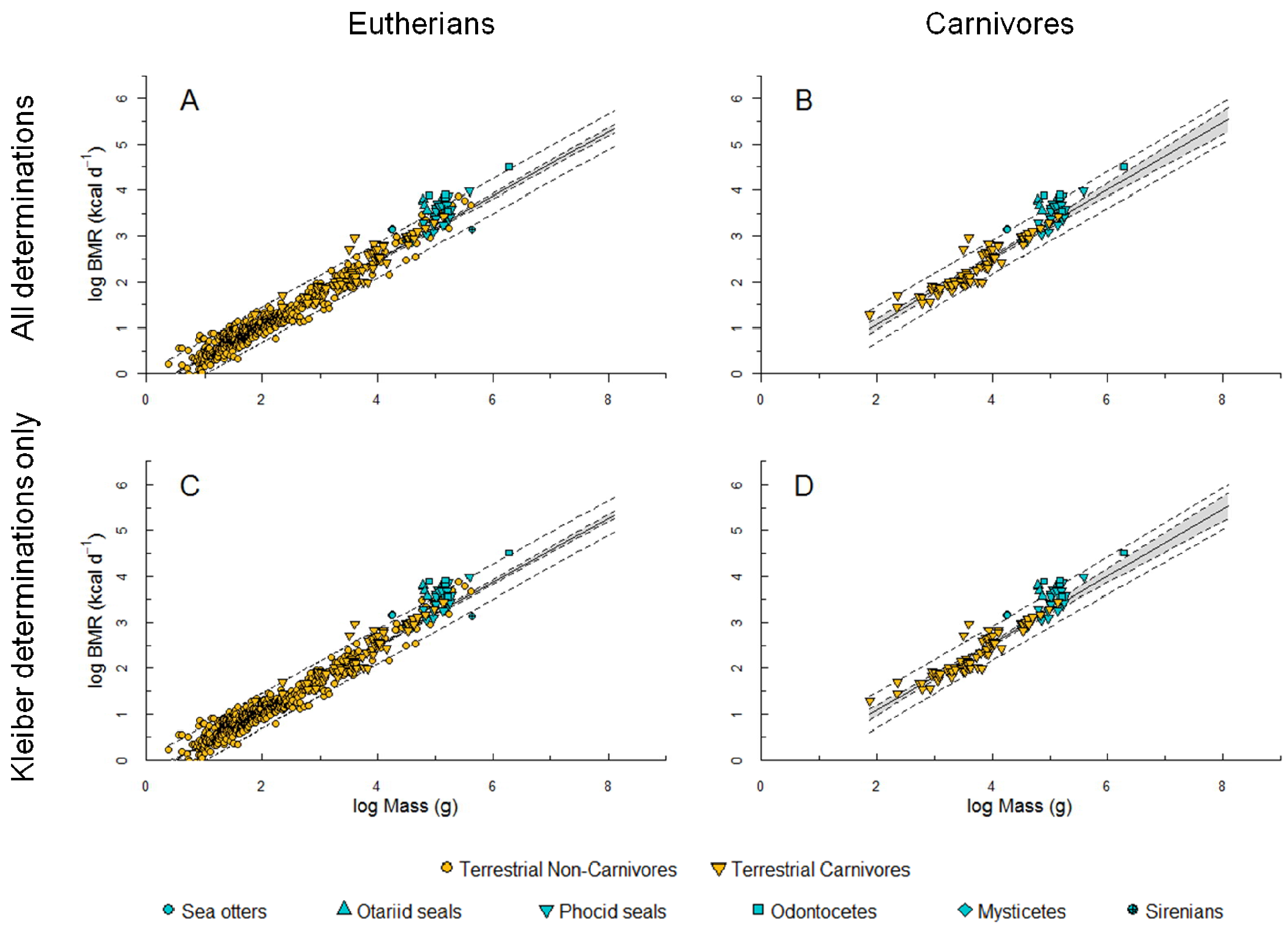

Eutherians
Carnivores
All determinations
Kleiber determinations only
A
B
C
D
log BMR (kcal d$^{-1}$)
0
1
2
3
4
5
6
log Mass (g)
0
2
4
6
8
● Terrestrial Non-Carnivores
▼ Terrestrial Carnivores
● Sea otters
▲ Otariid seals
▼ Phocid seals
■ Odontocetes
◆ Mysticetes
● Sirenians

**Figure 4.2. Field metabolic demands of mammals when data for marine mammals include non-empirical determinations (top row), and when data include only empirical determinations (bottom row).** The left column (A, C) shows comparisons among all eutherian mammals with regression lines bounded by 95% confidence intervals (grey shading bordered by dashed lines) and 95% prediction intervals (outer set of dashed lines) for terrestrial eutherians ($y = 187.8x^{0.72}$). The right column (B, D) shows comparisons among terrestrial carnivores and marine mammals with regression lines, 95% C.I. and 95% P.I. for terrestrial carnivores ($y = 178.1x^{0.77}$). Marine mammal FMR is predicted to be below that of terrestrial carnivores at body sizes above approximately 180 kg (red line). Note that, for display purposes, grams are the units of mass in the figures while the equations are for units of mass in kilograms as described in the text. Each data point represents an individual measurement.

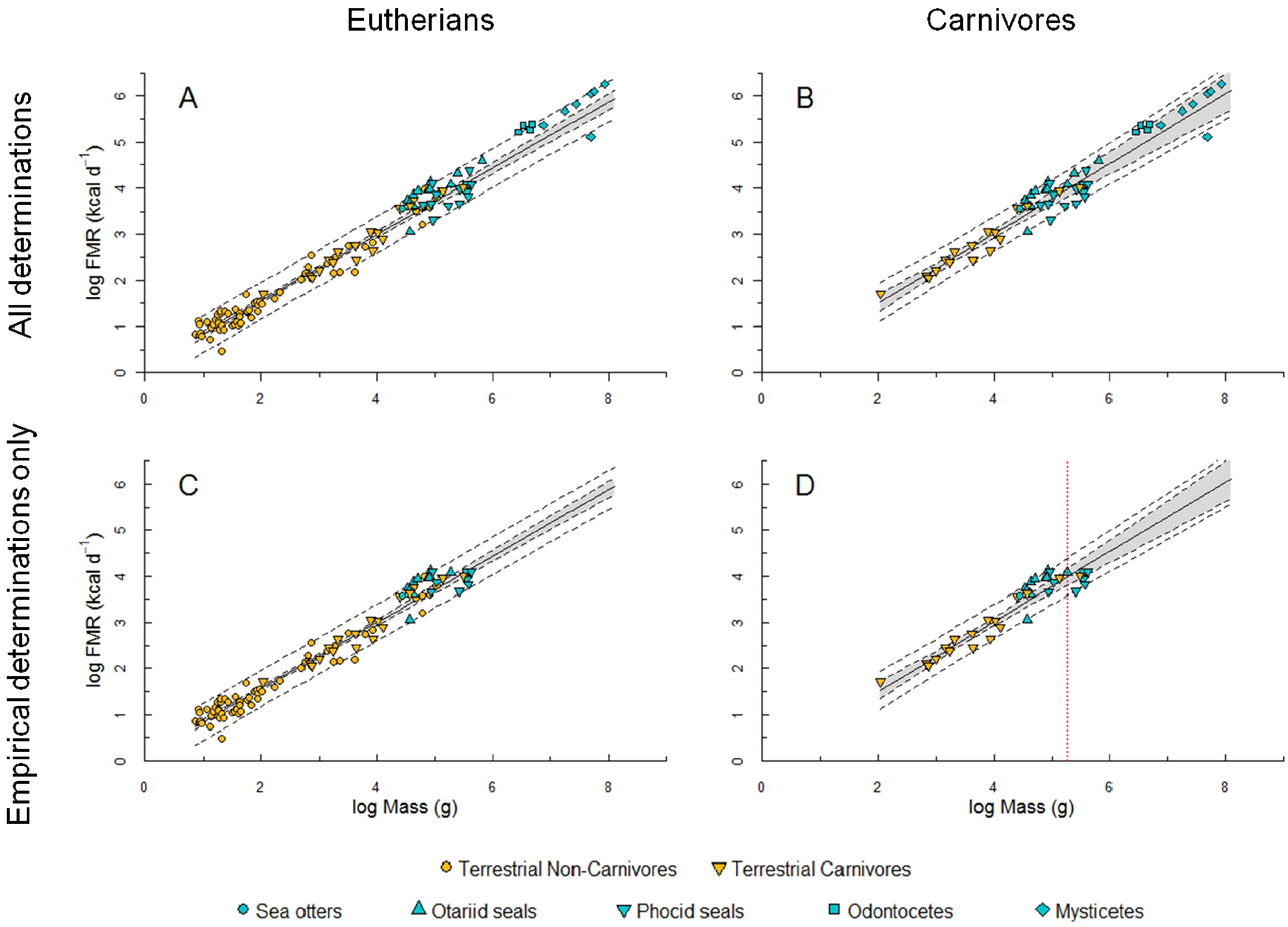
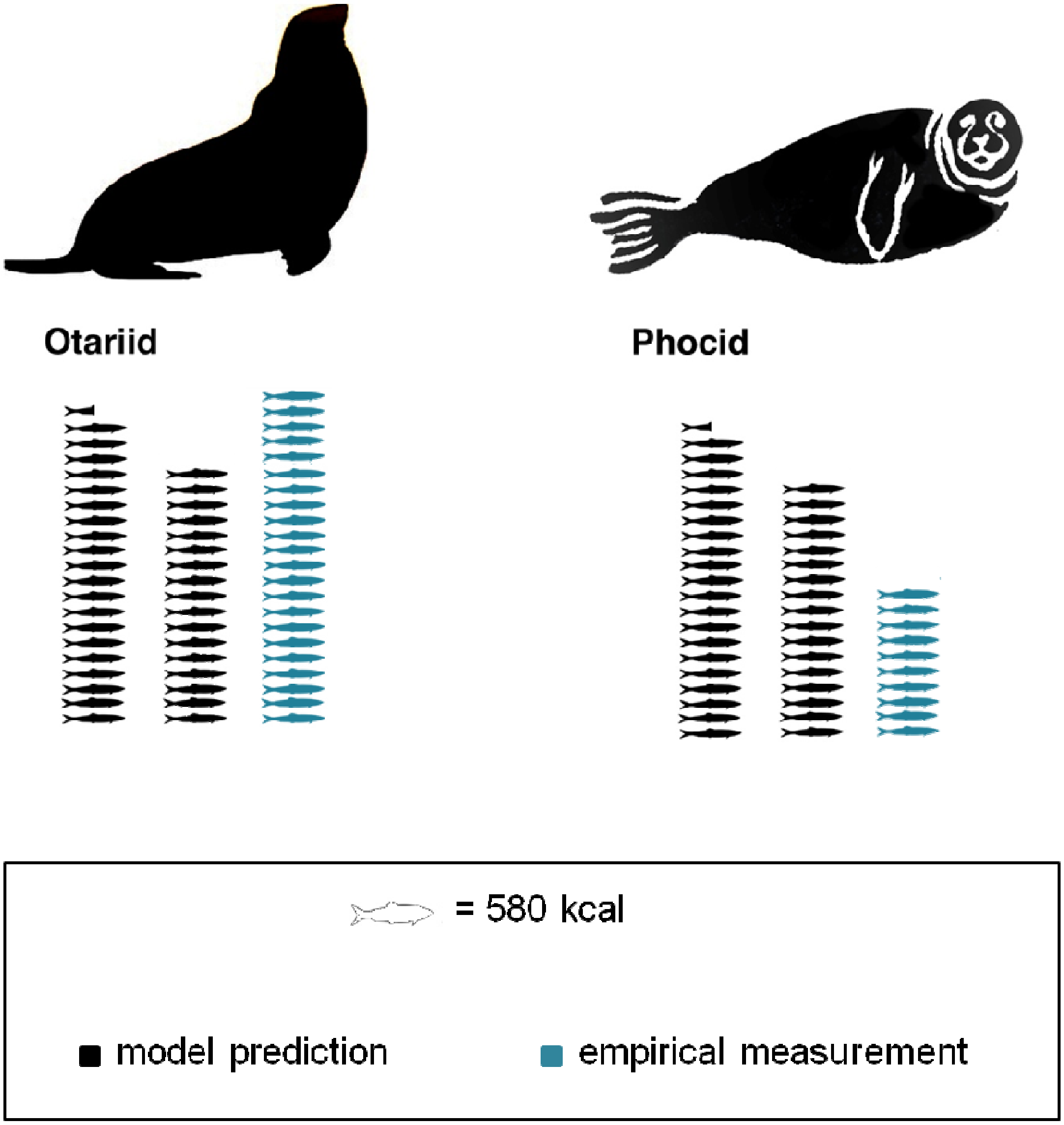

Eutherians
Carnivores
All determinations
Empirical determinations only
A
B
C
D
log FMR (kcal d$^{-1}$)
log Mass (g)
0
1
2
3
4
5
6
0
2
4
6
8
● Terrestrial Non-Carnivores
▼ Terrestrial Carnivores
● Sea otters
▲ Otariid seals
▼ Phocid seals
■ Odontocetes
◆ Mysticetes

**Figure 4.3. Model predictions of daily prey requirements compared to empirical measurements for a 200-kg otariid (13,000 kcal d$^{-1}$) and a 200-kg phocid seal (6,800 kcal d$^{-1}$).** Empirical measurements (blue fish) indicate phocid seals may have roughly half the prey energy requirements of otariid seals. Traditional models (left-most columns) based on the overrepresentation of otariids, and including extrapolated estimates for odontocetes and mysticete whales as well as data for immature seals, predict similar energy requirements of approximately 12,000 kcal d$^{-1}$. Prey requirements tend to be seriously overestimated for phocid seals, while only slightly underestimated for otariid seals. Newer model from this paper, eq. 4.1 (middle columns), predicts similar energy requirements of approximately 9,900 kcal d$^{-1}$, somewhat under- and overestimating prey requirements for otariid and phocid seals, respectively. In either case, data do not support a general model for all marine mammals that is appropriate for estimating the food consumption rates of individual species.

Otariid estimate is based on an average of empirical field metabolic rates for: Antarctic fur seals, *Arctocephalus gazelle* (Costa and Trillmich, 1988; Costa et al., 1989; Boyd and Duck, 1991; Arnould et al., 1996), northern fur seals, *Callorhinus ursinus* (Costa et al., 1985; Costa and Gentry, 1986), California sea lions, *Zalophus californianus* (Costa, 1991; Costa et al., 1991), and Australian sea lions, *Neophoca cinerea* (Costa, 1991; Costa and Gales, 2003). Phocid estimate is based on an average of empirical field metabolic rates for: Weddell seals, *Leptonychotes weddellii* (Kooyman et al., 1973; Kooyman et al., 1980; Kooyman et al., 1983; Castellini et al., 1992; Ponganis et al., 1993), harbor seals, *Phoca vitulina* (Bowen et al., 1992), and northern elephant seals, *Mirounga angustirostris* (Maresh et al., in review) . Number of prey fish were estimated assuming the energy density of a 0.55 kg Pacific herring (*Clupea pallasii*) (5.44 MJ kg$^{-1}$, OPR–NOAA Fisheries, 2012) and an 83% assimilation efficiency (Lavigne, 1982).


Otariid
Phocid
= 580 kcal
■ model prediction
■ empirical measurement

# Chapter 5

# Synthesis

## 5.1 Elephant seals and disturbance

The original motivation for the work I presented here was to contribute to efforts to understand how to mitigate the impacts of disruptive anthropogenic activities on marine mammals. My study was a small part of a much larger project (PCoD: Population Consequences of Disturbance) following the proximate physiological and behavioral responses of individuals to disturbances through to ultimate population-level effects. To answer a question like this requires knowledge on vital parameters at each level of biological organization (boxes in Fig. 5.1), but also on the transfer functions between each level (arrows in Fig. 5.1).

This sort of knowledge is not easy to come by even for the most tractable species let alone most marine mammals in the wild. So, as could be expected of a research project with origins at UC Santa Cruz, we decided to take a crack at the PCoD effort by starting with the northern elephant seal. The incredible long-term tracking program, research infrastructure, and unrivaled expertise available here provided me with not only a relatively accessible study species, but also an unusually rich dataset with which to work. However, it quickly became apparent that in order to answer questions regarding how resilient elephant seals are to anthropogenic disturbances at sea, some information gaps regarding the basic foraging ecology of this species needed to be filled. The most relevant questions regarding my part in the PCoD project revolved around the general concept of how elephant seals make a living at sea, specifically (1) How much does it cost, energetically speaking, to be an elephant seal? and (2) What are the typical behaviors and associated physiologies that underscore successful foraging in this species? Basically, my task was to fill in the boxes on the left-side of the flow chart in Fig. 5.1. so that ultimately we could address the question: (3) How resilient are elephant seals to at-sea disturbance?

The results of my work not only provided the information necessary to complete the northern elephant seal's part of the story in the larger PCoD effort, but they also allowed us to answer a long-standing but very fundamental question about the basic resource needs of this species. And yet again, the elephant seal proved itself to be one of the most extraordinary and intriguing animals on the planet. I have shown that, in their bioenergetics, northern elephant seals are doing something very different than most mammals, and also (probably) than most other marine mammals. Indeed, it is very clear that elephant seals do not conform to the traditional expectations of marine mammal prey-energy requirements, and it was this finding that motivated a re-inspection of these traditional expectations.

## 5.2 Marine mammals and paradigms

By virtue of their cryptic, far-ranging behaviors, marine mammals are less well-understood in many aspects of their biology than their terrestrial counterparts. Many studies are thus compelled to sideline marine mammals in comparative discussions, or use assumptions to fill in the information gaps. One such assumption is that marine mammals, by and large, should have elevated metabolic rates compared to terrestrial mammals. This assumption is based on measurements taken on a small subset of species, and its pervasiveness is surprising given its incompatibility with both an increasing numbers of studies demonstrating otherwise, and with the biodiversity of the animals themselves. As a group, marine mammals represent at least three separate lineages, cover a broad range of habitats and foraging strategies, and exhibit a wide variety of morphological and sensory adaptations. Indeed, the group of animals collectively known as "marine mammals" has no basis in taxonomic reality and is but a convenient catchall for a diverse group of organisms with an aquatic existence. Based on their diversity, we should not expect a uniform set of metabolic adaptations across the different groups.

While the results of my first two data chapters (Chs. 2, 3) emphasize elephant seals as perhaps the most extreme example, it is clear from the results of my third data chapter (Ch. 4) that numerous other species also do not conform to expectations of uniformly elevated metabolic rates in marine mammals. My work here demonstrates that while marine mammals as a group are certainly very different from terrestrial animals in many ways, they are not actually any different from other mammalian carnivores in their energy needs: metabolic energy demand is perhaps elevated on average relative to non-carnivores, but there is considerable intraspecies variability that underscores the diverse biologies of these animals that superficially resemble each other. This finding represents a serious challenge to what I see as a paradigm in need of reexamination, as marine mammals as a group are much more complex and much less generalizable in their bioenergetics than previously described.

## 5.3 New questions

It is my hope that my dissertation contributes to efforts to more robustly understand how marine mammals compare to other animals in their metabolic adaptations. I was able to show that northern elephant seals are one (extreme) example of numerous marine mammals whose metabolic energy demand is not in line with classical predictions. These results indicate that the energy needs of an aquatic animal are likely driven by some of the same extrinsic and intrinsic factors, and are subject to some of the same rules and constraints, as those of animals on land, although this is an area that requires further exploration. A new model identifying the most reliable predictors of prey-energy requirements in marine mammals has obvious practical applications for management and conservation efforts, but also could be particularly useful when working with data-deficient species.

My work also was able to demonstrate that anthropogenic disturbance to wild marine mammals can have serious impacts on behavior and foraging success, and this is notable given that elephant seals generally are considered to be a relatively hearty species. These results suggest that more sensitive species should be expected to experience the effects of at-sea disturbance more severely. As scientists who are intrigued and inspired by the animals we study, how do we apply some of the techniques and lessons learned here to these species, to learn more about how they work and predict how resilient they might be to increasing levels of human use and modification of their habitats? An understanding of an individual's basic energy needs represents a potentially powerful approach to forecasting a population's adaptive capacity, as evidenced by the growing interest in bioenergetics studies.

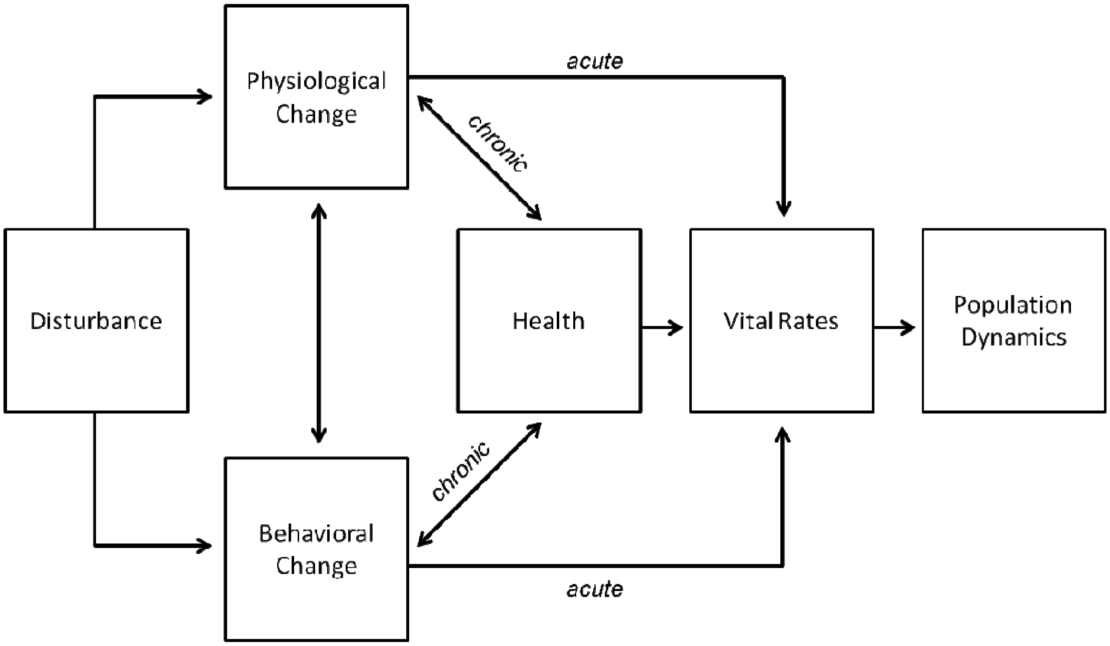


**Figure 5.1 Conceptual model of the links between changes in behavior and physiology, health, vital rates and population dynamics.** Changes in behavior and physiology due to acute disturbances will directly affect vital rates, while chronic disturbances will affect behavior and physiology and then health, before impacting vital rates. Changes in vital rates result in changes in population dynamics. Adapted from New et al. (in review).

# Appendices

## A.1.1 Basal metabolic rates: eutherian mammals

Body mass (kg) and basal metabolic rate (kcal $d^{-1}$) of eutherian mammals, with reference to original (Source 1) and review (Source 2) data sources. Measurement medium is noted (in air, in water, both, or not specified). Each individual determination was evaluated for conformity to Kleiber's (1975) criteria for measurements of basal metabolic rate in mammals, where

1 = post-prandial
2 = adult
3 = within thermal neutral zone
4 = resting (but not sleeping, sedated or restrained)

All data were used in comparisons labeled "All determinations" (Figs. 4.1A and 4.1C). Data obtained under measurement conditions not conforming to all four Kleiber criteria, as well as any non-empirical data (estimates), were excluded in comparisons labeled "Kleiber determinations only" (Figs. 4.1B and 4.1D).

## Marine Mammals

| Scientific Name | Common Name | Mass (kg) | BMR (kcal d⁻¹) | Measurement Medium | Kleiber's Criteria 1 | 2 | 3 | 4 | Source (1) | Source (2) |
|---|---|---|---|---|---|---|---|---|---|---|
| **Carnivores** | | | | | | | | | | |
| **Mustelidae** | | | | | | | | | | |
| *Enhydra lutris* | Sea otter | 17.3 | 1406.1 | water | Y | Y | Y | Y | 49 | |
| | | 18.0 | 1500.5 | both | Y | Y | Y | Y | 192 | 4 |
| | | 18.4 | 1406.0 | water | Y | Y | Y | Y | 50 | |
| **Mysticeti** | | | | | | | | | | |
| *Balaenoptera musculus* | Blue whale | 122000.0 | 1059737.4 | estimate | - | - | - | - | 152 | 2 |
| *Balaenoptera physalus* | Fin whale | 70000.0 | 534132.9 | estimate | - | - | - | - | 152 | 2 |
| *Eschrichtius robustus* | Gray whale | 1817.0 | 17366.4 | water | ? | N | Y | Y | 254 | 3 |
| | | 1987.0 | 20145.0 | water | ? | N | Y | Y | 254 | 3 |
| | | 2456.0 | 21534.3 | water | ? | N | Y | Y | 254 | 3 |
| | | 2555.0 | 37511.4 | water | ? | N | Y | Y | 254 | 3 |
| | | 2697.0 | 27786.2 | water | ? | N | Y | Y | 254 | 3 |
| | | 2882.0 | 27786.2 | water | ? | N | Y | Y | 254 | 3 |
| | | 3265.0 | 50709.9 | water | ? | N | Y | Y | 254 | 3 |
| | | 3478.0 | 76412.2 | water | ? | N | Y | Y | 254 | 3 |
| | | 5509.0 | 116702.2 | water | ? | N | Y | Y | 254 | 3 |
| **Odobenidae** | | | | | | | | | | |
| *Odobenus rosmarus* | Walrus | 62.0 | 2900.0 | air | Y | N | Y | Y | 130 | 3 |
| | | 66.0 | 2950.0 | air | Y | N | Y | Y | 130 | 3 |
| **Odontoceti** | | | | | | | | | | |
| *Globicephala scammoni* | Short-finned pilot whale | 450.0 | 43728.6 | water | ? | N | ? | N | 203 | 3 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Lagenorhynchus obliquidens* | Pacific white-sided dolphin | 80.0 | 7700.0 | water | Y | Y | Y | Y | 216 | |
| *Orcinus orca* | Killer whale | 1880.0 | 32374.0 | water | Y | Y | Y | Y | 69 | |
| | | 2692.0 | 145086.9 | estimate | - | - | - | - | 143 | 9 |
| | | 3550.0 | 220149.7 | estimate | - | - | - | - | 3 | 9 |
| | | 3750.0 | 180109.3 | estimate | - | - | - | - | 143 | 9 |
| *Phocoena phocoena* | Harbor porpoise | 16.0 | 1260.0 | water | Y | N | ? | ? | 135 | 3 |
| | | 19.0 | 3126.0 | water | ? | N | ? | N | 134 | 3 |
| | | 26.0 | 2195.0 | water | Y | N | ? | ? | 135 | 3 |
| | | 26.0 | 2639.7 | water | ? | N | ? | N | 134 | 4 |
| | | 31.0 | 2512.3 | water | ? | N | ? | N | 134 | 4 |
| | | 33.0 | 2360.0 | water | Y | N | ? | ? | 135 | 3 |
| *Stenella coeruleoalba* | Striped dolphin | 150.0 | 8100.0 | water | Y | Y | Y | Y | 136 | 1 |
| *Stenella longirostris* | Spinner dolphin | 65.0 | 3520.0 | estimate | - | - | - | - | 12 | |
| | | 67.7 | 2488.0 | water | ? | N | ? | N | 97 | 3 |
| *Tursiops truncatus* | Bottlenose dolphin | 115.0 | 3360.0 | water | Y | N | ? | ? | 135 | 3 |
| | | 128.0 | 6220.0 | water | ? | ? | Y | Y | 216 | 3 |
| | | 145.0 | 6872.3 | water | Y | Y | Y | Y | 267 | 2 |
| | | 145.0 | 9030.5 | water | ? | Y | ? | N | 127 | 3 |
| | | 148.6 | 6740.7 | water | Y | Y | Y | Y | 268 | |
| | | 150.0 | 4320.0 | water | Y | N | ? | ? | 135 | 3 |
| | | 156.0 | 6738.2 | water | ? | Y | ? | ? | 98 | 3 |
| | | 160.0 | 3500.0 | water | Y | Y | Y | Y | 134 | 7 |
| | | 170.0 | 6946.6 | water | ? | Y | ? | N | 127 | 3 |
| | | 200.0 | 6807.6 | water | ? | Y | ? | N | 127 | 3 |
| | | 213.0 | 5830.0 | water | Y | Y | ? | ? | 135 | 3 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Otariidae** | | | | | | | | | | |
| *Callorhinus ursinus* | Northern fur seal | 5.5 | 72.3 | water | Y | N | Y | N | 14 | 3 |
| | | 5.5 | 371.7 | water | Y | N | N | N | 14 | 3 |
| | | 9.4 | 761.8 | air | Y | N | Y | Y | 189 | 3 |
| | | 14.0 | 1167.0 | air | Y | N | Y | Y | 189 | 3 |
| | | 21.0 | 1410.2 | air | Y | N | Y | Y | 189 | 3 |
| | | 32.0 | 2500.0 | air | Y | N | Y | ? | 130 | 3 |
| *Eumetopias jubatus* | Steller sea lion | 13.0 | 740.0 | air | Y | N | Y | Y | 130 | 3 |
| | | 20.0 | 1000.0 | air | Y | N | Y | Y | 130 | 3 |
| | | 21.0 | 900.0 | air | Y | N | Y | Y | 130 | 3 |
| | | 111.3 | 5605.9 | air | Y | N | Y | Y | 222 | |
| | | 140.0 | 4201.3 | air | Y | N | Y | Y | 222 | |
| | | 173.7 | 10072.5 | water | Y | Y | Y | Y | 74 | |
| *Zalophus californianus* | CA sea lion | 28.2 | 2223.5 | air | Y | N | Y | ? | 164 | 3 |
| | | 30.0 | 3853.7 | water | Y | N | Y | Y | 146 | 3 |
| | | 33.0 | 1663.2 | air | ? | N | Y | Y | 237 | 3 |
| | | 34.9 | 1759.4 | air | Y | N | Y | Y | 237 | 2 |
| | | 37.0 | 1864.8 | air | ? | N | Y | Y | 237 | 3 |
| | | 40.0 | 4412.8 | water | Y | N | Y | Y | 146 | 3 |
| | | 46.8 | 4289.5 | water | Y | N | Y | N | 210 | 3 |
| | | 54.8 | 2328.1 | air | Y | N | Y | ? | 164 | 3 |
| | | 61.5 | 2746.0 | air | Y | Y | Y | N | 164 | |
| | | 61.6 | 5807.3 | water | Y | Y | Y | Y | 150 | |
| | | 62.0 | 6251.9 | water | Y | Y | Y | Y | 51 | |
| | | 62.2 | 2778.8 | air | Y | N | Y | ? | 164 | 3 |
| | | 66.0 | 4690.2 | water | Y | Y | Y | Y | 124 | |
| | | 69.7 | 3145.1 | air | Y | N | Y | ? | 164 | 3 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 73.0 | 3591.4 | water | Y | Y | Y | Y | 150 | |
| | | 128.0 | 5717.3 | water | Y | Y | Y | Y | 124 | |
| **Phocidae** | | | | | | | | | | |
| *Halichoerus grypus* | Grey seal | 28.0 | 2045.7 | ? | Y | N | Y | Y | 273 | 3 |
| | | 29.0 | 1389.3 | water | Y | N | Y | N | 229 | 3 |
| | | 31.5 | 1940.9 | water | Y | N | Y | Y | 238 | |
| | | 33.7 | 2200.5 | water | Y | N | Y | Y | 238 | |
| | | 33.8 | 1812.6 | water | Y | N | Y | Y | 238 | |
| | | 34.0 | 1898.9 | water | Y | N | Y | Y | 238 | |
| | | 35.0 | 1689.8 | water | Y | N | Y | Y | 238 | |
| | | 38.0 | 2610.0 | ? | Y | N | Y | Y | 273 | 3 |
| | | 40.5 | 2200.0 | water | Y | N | Y | Y | 238 | |
| | | 50.0 | 118.1 | ? | Y | N | Y | Y | 76 | 3 |
| | | 70.0 | 2735.3 | ? | Y | N | Y | Y | 148 | |
| | | 82.0 | 2193.4 | ? | Y | N | Y | Y | 148 | |
| | | 85.0 | 3070.8 | ? | Y | N | Y | Y | 148 | |
| | | 91.8 | 3892.5 | air | Y | N | Y | Y | 15 | |
| | | 111.0 | 5143.0 | water | Y | Y | Y | Y | 238 | |
| | | 119.0 | 4554.8 | water | Y | Y | Y | Y | 238 | |
| | | 133.0 | 4656.4 | water | Y | Y | Y | Y | 238 | |
| | | 147.3 | 6012.0 | water | Y | Y | Y | Y | 238 | |
| | | 160.0 | 4801.1 | air | Y | Y | Y | Y | 75 | 2 |
| | | 170.0 | 7428.0 | water | Y | Y | Y | Y | 238 | |
| | | 170.0 | 2333.0 | ? | Y | Y | Y | Y | 148 | |
| | | 176.0 | 2649.0 | ? | Y | Y | Y | Y | 148 | |
| | | 178.0 | 2765.0 | ? | Y | Y | Y | Y | 148 | |
| | | 190.7 | 3892.5 | air | Y | Y | Y | Y | 15 | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Leptonychotes weddellii* | Weddell seal | 35.0 | 2361.8 | ? | Y | N | Y | Y | 73 | 3 |
| | | 355.0 | 10110.7 | water | N | Y | Y | Y | 38 | 2 |
| | | 388.5 | 9661.5 | water | Y | Y | Y | Y | 268 | |
| | | 425.0 | 14816.4 | water | ? | Y | Y | Y | 142 | 2 |
| *Mirounga angustirostris* | Elephant seal | 106.9 | 1701.9 | water | Y | N | Y | ? | 210 | 3 |
| *Monachus schauinslandi* | HI monk seal | 82.0 | 2802.0 | water | Y | N | Y | Y | 270 | |
| | | 140.0 | 1790.5 | air | Y | Y | Y | Y | 70 | 10 |
| *Pagophilus groenlandicus* | Harp seal | 17.0 | 800.0 | air | Y | N | Y | Y | 130 | 3 |
| | | 18.0 | 950.0 | air | Y | N | Y | Y | 130 | 3 |
| | | 25.0 | 2735.5 | ? | Y | N | Y | Y | 148 | |
| | | 29.0 | 1844.0 | ? | Y | N | Y | Y | 273 | 3 |
| | | 31.0 | 1857.3 | ? | Y | N | Y | Y | 273 | 3 |
| | | 32.2 | 2145.1 | ? | Y | N | Y | Y | 273 | 3 |
| | | 35.2 | 1762.3 | ? | Y | N | Y | Y | 273 | 3 |
| | | 35.4 | 1701.9 | both | Y | N | Y | N | 126 | 3 |
| | | 35.8 | 1928.0 | ? | Y | N | Y | Y | 273 | 3 |
| | | 41.7 | 1722.7 | both | Y | N | Y | N | 126 | 3 |
| | | 62.0 | 2503.1 | ? | Y | N | Y | Y | 148 | |
| | | 66.0 | 4102.9 | ? | Y | N | Y | Y | 148 | |
| | | 95.0 | 1253.5 | water | Y | Y | Y | Y | 106 | 2 |
| | | 95.0 | 1782.1 | water | Y | Y | Y | Y | 106 | 2 |
| | | 105.0 | 4158.9 | ? | Y | Y | Y | Y | 204 | 2 |
| | | 105.0 | 3561.1 | ? | Y | Y | Y | Y | 148 | |
| | | 105.0 | 2451.5 | ? | Y | Y | Y | Y | 148 | |
| | | 140.7 | 2807.0 | water | Y | Y | Y | Y | 78 | |
| | | 150.0 | 3403.8 | water | Y | Y | Y | Y | 79 | |
| *Phoca fasciata* | Ribbon seal | 54.0 | 2438.2 | air | Y | N | Y | ? | 130 | 4 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Phoca vitulina* | Harbor seal | 11.0 | 1018.8 | air | Y | N | Y | N | 187 | 3 |
| | | 13.0 | 1113.8 | water | Y | N | Y | N | 188 | 3 |
| | | 19.0 | 580.0 | air | Y | N | Y | Y | 130 | 3 |
| | | 19.4 | 2063.1 | both | Y | N | Y | N | 126 | 3 |
| | | 20.0 | 1389.3 | both | Y | N | Y | N | 103 | 3 |
| | | 22.7 | 1314.1 | air | Y | N | Y | N | 187 | 3 |
| | | 22.8 | 1444.9 | both | Y | N | Y | N | 103 | 3 |
| | | 24.4 | 1507.4 | both | Y | N | Y | N | 103 | 3 |
| | | 25.1 | 1437.9 | both | Y | N | Y | N | 103 | 3 |
| | | 26.8 | 1597.7 | both | Y | N | Y | N | 126 | 3 |
| | | 27.4 | 1506.2 | both | ? | N | Y | N | 103 | 4 |
| | | 27.4 | 1479.6 | both | Y | N | Y | N | 103 | 3 |
| | | 29.1 | 1400.1 | air | Y | N | ? | Y | 99 | 2 |
| | | 31.3 | 1847.8 | both | Y | N | Y | N | 126 | 3 |
| | | 31.7 | 1521.3 | both | Y | N | Y | N | 103 | 3 |
| | | 32.0 | 3153.3 | water | Y | N | Y | Y | 269 | 2 |
| | | 32.8 | 1646.3 | both | Y | N | Y | N | 103 | 3 |
| | | 33.0 | 1139.9 | water | Y | N | Y | Y | 55 | 2 |
| | | 35.6 | 1993.7 | both | Y | N | Y | N | 126 | 3 |
| | | 40.0 | 1875.6 | water | N | N | Y | N | 52 | 3 |
| | | 41.0 | 2306.3 | both | Y | N | Y | N | 126 | 3 |
| | | 45.0 | 1736.6 | water | N | N | Y | N | 52 | 3 |
| | | 63.0 | 1961.8 | water | Y | Y | Y | Y | 55 | 2 |
| | | 98.0 | 2684.5 | air | Y | Y | Y | Y | 164 | 2 |
| | | 98.0 | 2422.0 | air | Y | Y | Y | N | 164 | 3 |
| *Pusa hispida* | Ringed seal | 32.0 | 730.5 | ? | Y | Y | Y | Y | 148 | |
| | | 38.5 | 797.4 | ? | Y | Y | Y | Y | 148 | |

|  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  | 41.0 | 806.9 | ? | Y | Y | Y | Y | 148 |  |
|  |  | 47.5 | 1084.1 | ? | Y | Y | Y | Y | 148 |  |
|  |  | 72.0 | 1104.5 | ? | Y | Y | Y | Y | 148 |  |
| **Non-Carnivores** |  |  |  |  |  |  |  |  |  |  |
| **Sirenidae** |  |  |  |  |  |  |  |  |  |  |
| *Trichechus manatus* | W. Indian manatee | 84.0 | 895.0 | water | Y | Y | Y | Y | 77 |  |
|  |  | 170.0 | 1518.7 | water | Y | Y | Y | Y | 77 |  |
|  |  | 427.7 | 1383.4 | water | Y | Y | Y | Y | 125 |  |
|  |  | 250.0 | 7312.2 | water (?) | ? | Y | ? | N | 231 |  |

## Terrestrial Mammals

| Scientific Name | Common Name | Mass (kg) | BMR (kcal $d^{-1}$) | Measurement Medium | Kleiber's Criteria |  |  |  | Source (1) | Source (2) |
|---|---|---|---|---|---|---|---|---|---|---|
|  |  |  |  |  | 1 | 2 | 3 | 4 |  |  |
| **Carnivores** |  |  |  |  |  |  |  |  |  |  |
| **Ailuridae** |  |  |  |  |  |  |  |  |  |  |
| *Ailurus fulgens* | Red panda | 5.7 | 101.7 | air | Y | Y | Y | Y | 181 | 8 |
| **Canidae** |  |  |  |  |  |  |  |  |  |  |
| *Alopex lagopus* | Arctic fox | 3.6 | 159.1 | air | Y | Y | Y | Y | 37 | 8 |
| *Alopex lagopus (?)* | White fox | 4.0 | 936.0 | air | Y | Y | Y | Y | 230 |  |
| *Canis latrans* | Coyote | 10.0 | 311.0 | air | Y | Y | Y | Y | 86 | 8 |
| *Canis mesomelas* | Black-backed jackal | 7.7 | 446.9 | air | Y | Y | Y | Y | 60 | 8 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Cerdocyon thous* | Crab-eating fox | 5.4 | 176.5 | air | Y | Y | Y | Y | 108 | 8 |
| *Fennecus zerda* | Fennec fox | 1.2 | 67.5 | air | ? | Y | Y | Y | 163 | 8 |
| *Lycaon pictus* | African painted dog | 8.7 | 678.7 | air | ? | Y | Y | Y | 249 | 4 |
| *Vulpes macrotis* | Swift fox | 1.8 | 102.7 | air | Y | Y | Y | Y | 86 | 8 |
| | | | | | | | | | | |
| **Felidae** | | | | | | | | | | |
| *Acinonyx jubatus* | Cheetah | 34.0 | 905.4 | air | Y | Y | Y | Y | 182 | |
| | | 37.9 | 1039.9 | air | Y | Y | Y | Y | 182 | 8 |
| | | 41.8 | 1180.8 | air | Y | Y | Y | Y | 182 | |
| *Herpailurus yaguarondi* | Jaguarundi | 3.9 | 135.0 | air | Y | Y | Y | Y | 182 | |
| | | 8.4 | 201.1 | air | Y | Y | Y | Y | 182 | 8 |
| *Leopardus pardalis* | Ocelot | 10.5 | 362.0 | air | Y | Y | Y | Y | 182 | 8 |
| *Leopardus wiedii* | Margay | 3.0 | 100.7 | air | Y | Y | Y | Y | 182 | |
| | | 3.6 | 108.5 | air | Y | Y | Y | Y | 182 | 8 |
| | | 4.1 | 130.1 | air | Y | Y | Y | Y | 182 | |
| *Leptailurus serval* | Serval | 10.1 | 363.2 | air | Y | Y | Y | Y | 182 | 8 |
| *Lynx rufus* | Bobcat | 6.9 | 395.3 | air | Y | Y | Y | Y | 182 | |
| | | 8.5 | 431.4 | air | Y | Y | Y | Y | 182 | |
| | | 9.4 | 488.6 | air | Y | Y | Y | Y | 182 | 8 |
| | | 12.8 | 612.0 | air | Y | Y | Y | Y | 182 | |
| *Panthera leo* | Lion | 98.0 | 1962.9 | air | Y | Y | Y | Y | 182 | 8 |
| *Panthera onca* | Jaguar | 31.8 | 949.9 | air | Y | Y | Y | Y | 182 | |
| | | 50.4 | 1295.4 | air | Y | Y | Y | Y | 182 | 8 |
| | | 69.0 | 1485.9 | air | Y | Y | Y | Y | 182 | |
| *Panthera tigris* | Tiger | 137.9 | 2778.0 | air | Y | Y | Y | Y | 182 | 8 |
| *Puma concolor* | Mountain lion | 32.4 | 986.6 | air | Y | Y | Y | Y | 182 | |
| | | 32.5 | 970.8 | air | Y | Y | Y | Y | 182 | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 37.2 | 1023.7 | air | Y | Y | Y | Y | 182 | 8 |
| | | 40.9 | 1179.1 | air | Y | Y | Y | Y | 182 | |
| | | 42.9 | 904.0 | air | Y | Y | Y | Y | 182 | |
| **Herpestidae** | | | | | | | | | | |
| *Galerella sanguinea* | Slender mongoose | 0.54 | 47.5 | air | Y | Y | Y | Y | 133 | 8 |
| *Herpestes javanicus* | Small Asian mongoose | 0.61 | 46.7 | air | ? | Y | Y | Y | 72 | 4, 8 |
| *Suricata suricatta* | Meerkat | 0.85 | 35.9 | air | ? | Y | Y | Y | 197 | 8 |
| **Hyaenidae** | | | | | | | | | | |
| *Hyaena hyaena* | Striped hyena | 34.3 | 663.2 | air | Y | Y | Y | Y | 182 | 8 |
| *Proteles cristata* | Aardwolf | 7.7 | 223.2 | air | Y | Y | Y | Y | 178 | |
| | | 7.8 | 213.5 | air | Y | Y | Y | Y | 1 | 6 |
| | | 8.1 | 254.0 | air | Y | Y | Y | Y | 1 | 6, 8 |
| **Mephitidae** | | | | | | | | | | |
| *Spilogale putorius* | Eastern spotted skunk | 0.62 | 34.7 | air | Y | Y | Y | Y | 141 | 8 |
| **Mustelidae** | | | | | | | | | | |
| *Eira barbara* | Tayra | 3.0 | 141.4 | air | Y | Y | Y | Y | 181 | 8 |
| *Gulo gulo* | Wolverine | 12.7 | 659.3 | air | Y | Y | Y | Y | 129 | 4, 8 |
| *Lutra lutra* | European otter | 10.0 | 521.0 | air | Y | Y | Y | Y | 129 | 8 |
| *Martes americana* | American marten | 0.90 | 68.9 | air | Y | Y | Y | Y | 272 | 8 |
| | | 1.0 | 79.3 | air | Y | Y | Y | Y | 272 | 4 |
| *Martes martes* | European pine marten | 0.92 | 83.0 | air | Y | Y | Y | Y | 129 | 4, 8 |
| *Meles meles* | European badger | 11.0 | 345.4 | air | Y | Y | Y | Y | 129 | 4, 8 |
| *Mustela erminea* | Stoat | 0.075 | 19.1 | air | Y | Y | Y | Y | 36 | 8 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | 0.23 | 49.4 | air | Y | Y | Y | Y | 36 | 4 |
| *Mustela frenata* | Long-tailed weasel | 0.22 | 27.9 | air | Y | Y | Y | Y | 31 | 8 |
| *Taxidea taxus* | American badger | 9.0 | 312.6 | air | ? | Y | Y | ? | 101 | 8 |
| **Procyonidae** | | | | | | | | | | |
| *Bassariscus sumichrasti* | Cacomistle | 1.3 | 73.4 | air | Y | Y | Y | Y | 42 | 5, 8 |
| *Nasua nasua* | South American coati | 3.7 | 118.7 | air | Y | Y | Y | Y | 43 | 8 |
| | | 4.0 | 114.8 | air | Y | Y | Y | Y | 43 | 8 |
| *?* | Coati | 3.2 | 521.6 | air | Y | Y | Y | Y | 230 | |
| *Potos flavus* | Kinkajou | 2.0 | 85.3 | air | Y | Y | Y | Y | 181 | |
| | | 2.3 | 92.2 | air | Y | Y | Y | Y | 193 | 4, 8 |
| *Procyon cancrivorus* | Crab-eating raccoon | 1.2 | 53.7 | air | Y | Y | Y | Y | 230 | 8 |
| *Procyon lotor* | Raccoon | 3.7 | 144.9 | air | Y | Y | Y | Y | 43 | 5 |
| | | 6.5 | 216.8 | air | Y | Y | Y | Y | 181 | |
| **Ursidae** | | | | | | | | | | |
| *Melursus ursinus* | Sloth bear | 6.7 | 97.7 | air | Y | Y | Y | Y | 180 | 8 |
| **Viverridae** | | | | | | | | | | |
| *Arctictis binturong* | Binturong | 14.3 | 264.5 | air | Y | Y | Y | Y | 178 | 4, 8 |
| *Arctogalidia trivirgata* | Small-toothed palm civet | 2.0 | 64.0 | air | Y | Y | Y | Y | 181 | 8 |
| *Fossa fossana* | Malagasy civet | 2.3 | 104.9 | air | Y | Y | Y | Y | 181 | 8 |
| *Genetta tigrina* | Cape genet | 1.7 | 86.5 | air | Y | Y | Y | Y | 107 | 8 |
| *Nandinia binotata* | African palm civet | 4.3 | 99.9 | air | Y | Y | Y | Y | 178 | 8 |
| *Paradoxurus hermaphroditus* | Asian palm civet | 3.2 | 88.0 | air | Y | Y | Y | Y | 181 | 8 |
| | | 3.4 | 82.9 | air | Y | Y | Y | Y | 178 | |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Non-Carnivores** | | | | | | | | | | |
| **Afrosoricida** | | | | | | | | | | |
| *Amblysomus hottentotus* | Hottentot golden mole | 0.070 | 9.8 | air | Y | Y | Y | Y | 156 | 8 |
| *Chrysochloris asiatica* | Cape golden mole | 0.044 | 6.0 | air | Y | Y | Y | Y | 271 | 8 |
| *Echinops telfairi* | Lesser hedgehog tenrec | 0.12 | 15.5 | air | Y | Y | Y | Y | 156 | 8 |
| *Geogale aurita* | Large-eared tenrec | 0.007 | 0.89 | air | Y | Y | Y | Y | 243 | 8 |
| *Hemicentetes semispinosus* | Lowland streaked tenrec | 0.12 | 7.9 | air | Y | Y | Y | Y | 244 | 8 |
| *Limnogale mergulus* | Web-footed tenrec | 0.078 | 6.5 | air | Y | Y | Y | Y | 245 | 8 |
| *Microgale cowani* | Cowan's shrew tenrec | 0.012 | 3.7 | air | Y | Y | Y | Y | 242 | 8 |
| *Microgale dobsoni* | Dobson's shrew tenrec | 0.045 | 6.5 | air | Y | Y | Y | Y | 242 | 8 |
| *Microgale talazaci* | Talazac's shrew tenrec | 0.044 | 5.0 | air | Y | Y | Y | Y | 242 | 8 |
| *Nasua narica* | White-nosed coati | 3.7 | 139.8 | air | Y | Y | Y | Y | 181 | 8 |
| *Orycteropus afer* | Aardvark | 48.0 | 711.3 | air | Y | Y | Y | Y | 177 | 8 |
| *Setifer setosus* | Greater hedgehog tenrec | 0.53 | 14.1 | air | Y | Y | Y | Y | 175 | 8 |
| *Tenrec ecaudatus* | Tailless tenrec | 0.65 | 15.1 | air | Y | Y | Y | Y | 56 | 8 |
| **Artiodactyla** | | | | | | | | | | |
| *Alces alces* | Moose | 325.0 | 5953.1 | air | Y | Y | Y | Y | 213 | 8 |
| *Antilocapra americana* | Pronghorn | 37.8 | 1078.9 | air | Y | Y | Y | Y | 261 | 8 |
| *Camelus dromedarius* | Dromedary | 407.0 | 4712.1 | air | Y | Y | Y | Y | 228 | 4 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Capra* | Some kind of goat | 36.0 | 791.9 | air | Y | Y | Y | Y | 28 | 4 |
| *Capreolus capreolus* | Roe deer | 21.5 | 961.9 | air | Y | Y | Y | Y | 258 | 8 |
| *Cervus elaphus* | Red deer | 58.0 | 1880.2 | air | Y | Y | Y | Y | 27 | 4 |
| *Connochaetes taurinus* | Blue wildebeest | 140.0 | 3241.7 | air | Y | Y | Y | Y | 248 | 4 |
| | | 196.5 | 4774.8 | air | Y | Y | Y | Y | 220 | 8 |
| *Kobus ellipsiprymnus* | Waterbuck | 100.0 | 3126.0 | air | Y | Y | Y | Y | 250 | 4 |
| *Odocoileus virginianus* | White-tailed deer | 58.6 | 2964.9 | air | Y | Y | Y | Y | 236 | 8 |
| *Oreamnos americanus* | Mountain goat | 32.0 | 963.3 | air | Y | Y | Y | Y | 144 | 4 |
| *Ovis canadensis* | Bighorn sheep | 69.1 | 2213.7 | air | Y | Y | Y | Y | 39 | 8 |
| *Pecari tajacu* | Collared peccary | 20.5 | 688.3 | air | Y | Y | Y | Y | 276 | 8 |
| *Rangifer tarandus* | Reindeer | 94.0 | 2720.7 | air | Y | Y | Y | Y | 168 | 4 |
| *Tragelaphus oryx* | Common eland | 150.0 | 4167.9 | air | Y | Y | Y | Y | 247 | 4 |
| **Chiroptera** | | | | | | | | | | |
| *Anoura caudifera* | Tailed tailless bat | 0.011 | 4.9 | air | Y | Y | Y | Y | 171 | 8 |
| *Antrozous pallidus* | Pallid bat | 0.022 | 2.2 | air | Y | Y | Y | Y | 151 | 8 |
| *Artibeus concolor* | Brown fruit-eating bat | 0.020 | 4.6 | air | Y | Y | Y | Y | 171 | 4 |
| *Artibeus fimbriatus* | Fringed fruit-eating bat | 0.064 | 9.0 | air | Y | Y | Y | Y | 53 | 8 |
| *Artibeus jamaicensis* | Jamaican fruit bat | 0.045 | 8.9 | air | Y | Y | Y | Y | 171 | 8 |
| *Artibeus lituratus* | Great fruit-eating bat | 0.070 | 12.5 | air | Y | Y | Y | Y | 171 | 8 |
| *Carollia perspicillata* | Seba's short-tailed bat | 0.015 | 5.0 | air | Y | Y | Y | Y | 171 | 8 |
| *Chalinolobus gouldii* | Gould's wattled bat | 0.018 | 2.9 | air | Y | Y | Y | Y | 120 | 8 |

|  |  |  |  |  |  |  |  |  |  |  |
|---|---|---|---|---|---|---|---|---|---|---|
| *Chiroderma doriae* | Brazilian big-eyed bat | 0.020 | 3.6 | air | Y | Y | Y | Y | 53 | 8 |
| *Chrotopterus auritus* | Big-eared woolly bat | 0.096 | 16.4 | air | Y | Y | Y | Y | 171 | 8 |
| *Cynopterus brachyotis* | Lesser short-nosed fruit bat | 0.037 | 5.5 | air | Y | Y | Y | Y | 183 | 8 |
| *Desmodus rotundus* | Common vampire bat | 0.029 | 4.0 | air | Y | Y | Y | Y | 171 | 8 |
| *Diaemus youngi* | White-winged vampire bat | 0.037 | 4.3 | air | Y | Y | Y | Y | 171 | 8 |
| *Diphylla ecaudata* | Hairy-legged vampire bat | 0.028 | 4.5 | air | Y | Y | Y | Y | 171 | 8 |
| *Dobsonia minor* | Lesser naked-backed fruit bat | 0.074 | 8.6 | air | Y | Y | Y | Y | 183 | 8 |
|  |  | 0.087 | 12.7 | air | Y | Y | Y | Y | 183 | 8 |
| *Dobsonia moluccensis* | Moluccan naked-backed fruit bat | 0.32 | 31.4 | air | Y | Y | Y | Y | 183 | 8 |
| *Dobsonia praedatrix* | New Britain naked-backed fruit bat | 0.18 | 16.5 | air | Y | Y | Y | Y | 183 | 8 |
| *Eonycteris spelaea* | Cave nectar bat | 0.052 | 5.6 | air | Y | Y | Y | Y | 183 | 8 |
| *Eptesicus fuscus* | Big brown bat | 0.010 | 2.4 | air | Y | Y | Y | Y | 80 | 8 |
| *Erophylla sezekorni* | Buffy flower bat | 0.016 | 2.1 | air | Y | Y | Y | Y | 219 | 8 |
| *Eumops perotis* | Western mastiff bat | 0.056 | 4.6 | air | Y | Y | Y | Y | 171 | 8 |
| *Glossophaga soricina* | Pallas's long-tongued bat | 0.010 | 3.4 | air | Y | Y | Y | Y | 171 | 8 |
| *Hipposideros galeritus* | Cantor's roundleaf bat | 0.009 | 1.1 | air | Y | Y | Y | Y | 184 | 8 |
| *Histiotus velatus* | Tropical big-eared brown bat | 0.011 | 1.8 | air | Y | Y | Y | Y | 171 | 8 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Leptonycteris curasoae* | Southern long-nosed bat | 0.022 | 5.1 | air | Y | Y | Y | Y | 171 | 8 |
| *Macroderma gigas* | Ghost bat | 0.15 | 16.1 | air | Y | Y | Y | Y | 171 | 8 |
| *Macroglossus minimus* | Long-tongued nectar bat | 0.016 | 2.1 | air | Y | Y | Y | Y | 183 | 8 |
| *Macrotus californicus* | California leaf-nosed bat | 0.012 | 1.7 | air | Y | Y | Y | Y | 8 | 8 |
| *Megaloglossus woermanni* | Woermann's bat | 0.012 | 2.5 | air | Y | Y | Y | Y | 156 | 8 |
| *Melonycteris melanops* | Black-bellied fruit bat | 0.053 | 5.0 | air | Y | Y | Y | Y | 183 | 8 |
| *Miniopterus australis* | Little bent-wing bat | 0.11 | 10.9 | air | Y | Y | Y | Y | 6 | 8 |
| *Miniopterus schreibersi* | Common bent-wing bat | 0.011 | 3.0 | air | Y | Y | Y | Y | 6 | 8 |
| *Molossus molossus* | Velvety free-tailed bat | 0.016 | 2.6 | air | Y | Y | Y | Y | 171 | 8 |
| *Monophyllus redmani* | Leach's single leaf bat | 0.009 | 1.3 | air | Y | Y | Y | Y | 219 | 8 |
| *Mormoops blainvillii* | Antillean ghost-faced bat | 0.009 | 0.93 | air | Y | Y | Y | Y | 219 | 8 |
| *Mormoops megalophylla* | Ghost-faced bat | 0.016 | 2.8 | air | Y | Y | Y | Y | 17 | 8 |
| *Myotis lucifugus* | Little brown bat | 0.005 | 1.0 | air | Y | Y | Y | Y | 80 | 8 |
| *Myotis nigricans* | Black myotis | 0.004 | 0.56 | air | Y | Y | Y | Y | 184 | 8 |
| *Natalus tumidirostris* | Trinidadian funnel-eared bat | 0.005 | 1.0 | air | Y | Y | Y | Y | 82 | 8 |
| *Noctilio albiventris* | Lesser bulldog bat | 0.027 | 3.7 | air | Y | Y | Y | Y | 171 | 8 |

| | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Noctilio leporinus* | Greater bulldog bat | 0.061 | 8.2 | air | Y | Y | Y | Y | 171 | 8 |
| *Nyctimene albiventer* | Common tube-nosed fruit bat | 0.031 | 3.2 | air | Y | Y | Y | Y | 183 | 8 |
| *Nyctimene cyclotis* | Round-eared tube-nosed fruit bat | 0.040 | 7.5 | air | Y | Y | Y | Y | 183 | 8 |
| *Nyctimene major* | Island tube-nosed fruit bat | 0.014 | 2.4 | air | Y | Y | Y | Y | 119 | 8 |
| *Nyctophilus geoffroyi* | Lesser long-eared bat | 0.008 | 1.3 | air | Y | Y | Y | Y | 121 | 8 |
| *Paranyctimene raptor* | Lesser tube-nosed fruit bat | 0.024 | 2.8 | air | Y | Y | Y | Y | 183 | 8 |
| *Peropteryx macrotis* | Lesser dog-like bat | 0.005 | 1.3 | air | Y | Y | Y | Y | 82 | 8 |
| *Phyllostomus discolor* | Pale spear-nosed bat | 0.033 | 5.5 | air | Y | Y | Y | Y | 171 | 8 |
| *Phyllostomus elongatus* | Lesser spear-nosed bat | 0.036 | 4.5 | air | Y | Y | Y | Y | 171 | 8 |
| *Phyllostomus hastatus* | Greater spear-nosed bat | 0.084 | 11.6 | air | Y | Y | Y | Y | 171 | 8 |
| *Platyrrhinus lineatus* | White-lined broad-nosed bat | 0.022 | 5.2 | air | Y | Y | Y | Y | 171 | 8 |
| *Plecotus auritus* | Brown long-eared bat | 0.010 | 1.4 | air | Y | Y | Y | Y | 169 | 8 |
| *Pteronotus davyi* | Davy's naked-backed bat | 0.009 | 1.8 | air | Y | Y | Y | Y | 17 | 8 |
| *Pteronotus parnellii* | Parnell's mustached bat | 0.019 | 3.6 | air | Y | Y | Y | Y | 17 | 8 |
| *Pteronotus personatus* | Wagner's mustached bat | 0.014 | 2.7 | air | Y | Y | Y | Y | 17 | 8 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| *Pteronotus quadridens* | Sooty mustached bat | 0.005 | 0.71 | air | Y | Y | Y | Y | 219 | 8 |
| *Pteropus giganteus* | Indian flying fox | 0.56 | 33.7 | air | Y | Y | Y | Y | 183 | 8 |
| *Pteropus hypomelanus* | Smally flying fox | 0.52 | 33.6 | air | Y | Y | Y | Y | 183 | 8 |
| *Pteropus poliocephalus* | Grey-headed flying fox | 0.60 | 36.7 | air | Y | Y | Y | Y | 183 | 8 |
| *Pteropus pumilus* | Little golden-mantled flying fox | 0.19 | 14.6 | air | Y | Y | Y | Y | 183 | 8 |
| *Pteropus rodricensis* | Rodrigues flying fox | 0.25 | 15.6 | air | Y | Y | Y | Y | 183 | 8 |
| *Pteropus scapulatus* | Little red flying fox | 0.36 | 28.1 | air | Y | Y | Y | Y | 171 | 8 |
| *Pteropus vampyrus* | Large flying fox | 1.0 | 93.1 | air | Y | Y | Y | Y | 183 | 8 |
| *Rhinonicteris aurantia* | Orange leaf-nosed bat | 0.008 | 1.9 | air | Y | Y | Y | Y | 6 | 8 |
| *Rhinophylla fischerae* | Fischer's little fruit bat | 0.009 | 1.9 | air | Y | Y | Y | Y | 171 | 8 |
| *Rhinophylla pumilio* | Dwarf little fruit bat | 0.009 | 2.2 | air | Y | Y | Y | Y | 171 | 8 |
| *Rousettus amplexicaudatus* | Geoffroy's rousette | 0.091 | 12.1 | air | Y | Y | Y | Y | 183 | 8 |
| *Rousettus egyptiacus* | Egyptian fruit bat | 0.15 | 14.2 | air | Y | Y | Y | Y | 183 | 8 |
| *Saccopteryx bilineata* | Greater sac-winged bat | 0.008 | 1.7 | air | Y | Y | Y | Y | 81 | 8 |
| *Small stenodermines* | Short-tailed fruit bat | 0.010 | 2.5 | air | Y | Y | Y | Y | 171 | 4 |
| *Sturnira lilium* | Little yellow-shouldered bat | 0.022 | 6.2 | air | Y | Y | Y | Y | 171 | 8 |
| *Sturnira tildae* | Tilda's yellow-shouldered bat | 0.020 | 4.6 | air | Y | Y | Y | Y | 53 | 8 |
| *Syconycteris australis* | Common blossom bat | 0.016 | 2.5 | air | Y | Y | Y | Y | 183 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Tadarida brasiliensis* | Mexican free-tailed bat | 0.017 | 2.3 | air | Y | Y | Y | Y | 80 | 8 |
| *Tonatia bidens* | Greater round-eared bat | 0.027 | 6.4 | air | Y | Y | Y | Y | 171 | 8 |
| *Uroderma bilobatum* | Tent-making bat | 0.016 | 3.7 | air | Y | Y | Y | Y | 171 | 8 |
| *Vampyressa pusilla* | Southern little yellow-eared bat | 0.009 | 2.2 | air | Y | Y | Y | Y | 53 | 8 |
| *Vampyrops lineatus* | White-lined bat | 0.022 | 3.7 | air | Y | Y | Y | Y | 171 | 4 |
| **Cingulata** | | | | | | | | | | |
| *Cabassous centralis* | Northern naked-tailed armadillo | 4.3 | 106.1 | air | Y | Y | Y | Y | 175 | 8 |
| *Chaetophractus nationi* | Andean hairy armadillo | 2.2 | 64.7 | air | Y | Y | Y | Y | 175 | 8 |
| *Chaetophractus vellerosus* | Screaming hairy armadillo | 1.1 | 35.5 | air | Y | Y | Y | Y | 175 | 8 |
| *Chaetophractus villosus* | Big hairy armadillo | 4.5 | 93.6 | air | Y | Y | Y | Y | 175 | 8 |
| *Dasypus novemcinctus* | Nine-banded armadillo | 3.5 | 100.2 | air | Y | Y | Y | Y | 175 | 8 |
| *Euphractus sexcinctus* | Six-banded armadillo | 8.2 | 143.2 | air | Y | Y | Y | Y | 175 | 8 |
| *Priodontes maximus* | Giant armadillo | 45.2 | 350.5 | air | Y | Y | Y | Y | 175 | 8 |
| *Tolypeutes matacus* | Southern three-banded armadillo | 1.2 | 24.3 | air | Y | Y | Y | Y | 175 | 8 |
| *Zaedyus pichiy* | Pichi | 1.7 | 45.5 | air | Y | Y | Y | Y | 175 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| **Erinaceomorpha** | | | | | | | | | | |
| *Atelerix albiventris* | Four-toed hedgehog | 0.45 | 17.2 | air | Y | Y | Y | Y | 175 | 8 |
| *Echinosorex gymnura* | Moonrat | 0.72 | 58.4 | air | Y | Y | Y | Y | 265 | 8 |
| *Erinaceus concolor* | Southern white-breasted hedgehog | 0.82 | 40.2 | air | Y | Y | Y | Y | 145 | 8 |
| *Erinaceus europaeus* | European hedgehog | 0.75 | 39.1 | air | Y | Y | Y | Y | 235 | 8 |
| *Hemiechinus aethiopicus* | Desert hedgehog | 0.45 | 13.0 | air | Y | Y | Y | Y | 235 | 8 |
| *Hemiechinus auritus* | Long-eared hedgehog | 0.40 | 17.6 | air | Y | Y | Y | Y | 235 | 8 |
| *Hylomys suillus* | Short-tailed gymnure | 0.058 | 7.0 | air | Y | Y | Y | Y | 83 | 8 |
| *Setifer setosus* | Greater hedgehog tenrec | 0.53 | 14.1 | air | Y | Y | Y | Y | 175 | 8 |
| **Hyracoidea** | | | | | | | | | | |
| *Dendrohyrax dorsalis* | Western tree hyrax | 2.2 | 87.0 | air | Y | Y | Y | Y | 156 | 8 |
| *Heterohyrax brucei* | Yellow-spotted rock hyras | 2.0 | 83.4 | air | Y | Y | Y | Y | 172 | 8 |
| *Procavia capensis* | Rock hyrax | 2.5 | 105.7 | air | Y | Y | Y | Y | 226 | 8 |
| **Lagomorpha** | | | | | | | | | | |
| *Lepus alleni* | Antelope jackrabbit | 3.0 | 191.0 | air | Y | Y | Y | Y | 172 | 8 |
| | | 3.4 | 175.2 | air | Y | Y | Y | Y | 114 | 4 |
| *Lepus americanus* | Snowshoe hare | 1.6 | 175.7 | air | Y | Y | Y | Y | 172 | 8 |
| *Lepus arcticus* | Arctic hare | 3.0 | 125.2 | air | Y | Y | Y | Y | 257 | 8 |
| *Lepus californicus* | Black-tailed jackrabbit | 2.0 | 129.0 | air | Y | Y | Y | Y | 114 | 4 |
| | | 2.3 | 151.8 | air | Y | Y | Y | Y | 256 | 8 |
| *Lepus timidus* | Mountain hare | 3.0 | 245.3 | air | Y | Y | Y | Y | 211 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Lepus townsendii* | White-tailed jackrabbit | 2.4 | 146.3 | air | Y | Y | Y | Y | 221 | 8 |
| *Ochotona dauurica* | Daurian pika | 0.13 | 28.8 | air | Y | Y | Y | Y | 259 | 8 |
| *Ochotona princeps* | American pika | 0.11 | 19.3 | air | Y | Y | Y | Y | 159 | 8 |
| *Oryctolagus cuniculus* | European rabbit | 2.0 | 132.0 | air | Y | Y | Y | Y | 102 | 8 |
| *Sylvilagus audubonii* | Desert cottontail | 0.67 | 50.7 | air | Y | Y | Y | Y | 113 | 8 |
| | | 0.70 | 51.2 | air | Y | Y | Y | Y | 113 | 4 |
| **Macroscelidea** | | | | | | | | | | |
| *Elephantulus brachyrhynchus* | Short-snouted elephant shrew | 0.05 | 5.1 | air | Y | Y | Y | Y | 175 | 8 |
| *Elephantulus edwardii* | Cape elephant shrew | 0.050 | 6.3 | air | Y | Y | Y | Y | 177 | 8 |
| *Elephantulus intufi* | Bushveld elephant shrew | 0.046 | 6.0 | air | Y | Y | Y | Y | 175 | 8 |
| *Elephantulus myurus* | Eastern rock elephant shrew | 0.063 | 7.7 | air | Y | Y | Y | Y | 158 | 8 |
| *Elephantulus rozeti* | North African elephant shrew | 0.045 | 5.5 | air | Y | Y | Y | Y | 158 | 8 |
| *Elephantulus rufescens* | Rufous elephant shrew | 0.053 | 6.6 | air | Y | Y | Y | Y | 177 | 8 |
| *Macroscelides proboscideus* | Short-eared elephant shrew | 0.039 | 6.1 | air | Y | Y | Y | Y | 225 | 8 |
| *Petrodromus tetradactylus* | Four-toed elephant shrew | 0.206 | 20.8 | air | Y | Y | Y | Y | 63 | 8 |
| **Pholidota** | | | | | | | | | | |
| *Manis crassicaudata* | Indian pangolin | 15.9 | 143.7 | air | Y | Y | Y | Y | 177 | 8 |
| *Manis javanica* | Sunda pangolin | 4.2 | 128.0 | air | Y | Y | Y | Y | 177 | 8 |
| *Manis pentadactyla* | Chinese pangolin | 3.6 | 77.3 | air | Y | Y | Y | Y | 105 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Manis tetradactyla* | Long-tailed pangolin | 1.4 | 26.5 | air | Y | Y | Y | Y | 105 | 8 |
| *Manis tricuspis* | Tree pangolin | 1.4 | 32.0 | air | Y | Y | Y | Y | 105 | 8 |
| | | 2.7 | 104.3 | air | Y | Y | Y | Y | 109 | 4 |
| **Pilosa** | | | | | | | | | | |
| *Bradypus variegatus* | Brown-throated sloth | 3.8 | 79.4 | air | Y | Y | Y | Y | 173 | 8 |
| *Choloepus hoffmanni* | Hoffmann's two-toed sloth | 3.8 | 69.8 | air | Y | Y | Y | Y | 172 | 8 |
| **Primates** | | | | | | | | | | |
| *Alouatta palliata* | Mantled howler | 4.7 | 237.9 | air | Y | Y | Y | Y | 190 | 8 |
| *Aotus trivirgatus* | Three-striped night monkey | 0.82 | 51.2 | air | Y | Y | Y | Y | 230 | 8 |
| *Arctocebus calabarensis* | Calabar angwantibo | 0.21 | 15.2 | air | Y | Y | Y | Y | 156 | 8 |
| *Callithrix jacchus* | Common marmoset | 0.19 | 17.6 | air | Y | Y | Y | Y | 179 | 8 |
| *Callithrix pygmaea* | Pygmy marmoset | 0.12 | 13.6 | air | Y | Y | Y | Y | 191 | 8 |
| *Cercopithecus mitis* | Blue monkey | 8.5 | 392.7 | air | Y | Y | Y | Y | 196 | 8 |
| *Cheirogaleus medius* | Fat-tailed dwarf lemur | 0.30 | 22.6 | air | Y | Y | Y | Y | 166 | 8 |
| *Colobus guereza* | Mantled guereza | 10.4 | 344.8 | air | Y | Y | Y | Y | 196 | 8 |
| *Erythrocebus patas* | Pata monkey | 3.0 | 123.6 | air | Y | Y | Y | Y | 162 | 8 |
| *Eulemur fulvus* | Common brown lemur | 2.3 | 86.4 | air | Y | Y | Y | Y | 54 | 8 |
| *Euoticus elegantulus* | Southern needle-clawed bushbaby | 0.26 | 25.0 | air | Y | Y | Y | Y | 156 | 8 |
| *Galago moholi* | Mohol bushbaby | 0.17 | 5.9 | air | Y | Y | Y | Y | 140 | 8 |
| *Galago senegalensis* | Senegal bushbaby | 0.17 | 15.9 | air | Y | Y | Y | Y | 140 | 8 |
| *Galagoides zanzibaricus* | Zanzibar bushbaby | 0.064 | 6.9 | air | Y | Y | Y | Y | 156 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Loris tardigradus* | Red slender loris | 0.28 | 14.8 | air | Y | Y | Y | Y | 197 | 8 |
| *Nycticebus coucang* | Sunda slow loris | 1.2 | 31.6 | air | Y | Y | Y | Y | 194 | 8 |
| *Otolemur crassicaudatus* | Brown greater galago | 0.95 | 47.7 | air | Y | Y | Y | Y | 156 | 8 |
| *Otolemur garnettii* | Northern greater galago | 1.3 | 81.5 | air | Y | Y | Y | Y | 224 | 8 |
| *Papio hamadryas* | Hamadryas baboon | 13.2 | 458.8 | air | Y | Y | Y | Y | 246 | 8 |
| *Periodicticus potto* | Potto | 1.0 | 41.7 | air | Y | Y | Y | Y | 110 | 4 |
| | | 0.96 | 37.8 | air | Y | Y | Y | Y | 110 | 8 |
| *Propithecus verreauxi* | Verreaux's sifaka | 3.3 | 77.6 | air | Y | Y | Y | Y | 224 | 8 |
| *Saguinus geoffroyi* | Geoffroy's tamarin | 0.22 | 27.1 | air | Y | Y | Y | Y | 230 | 8 |
| *Saimiri sciureus* | Common squirrel monkey | 0.87 | 92.7 | air | Y | Y | Y | Y | 156 | 8 |
| *Tarsius spectrum* | Spectral tarsier | 0.17 | 17.3 | air | Y | Y | Y | Y | 45 | 8 |
| *Tarsius syrichta* | Philippine tarsier | 0.11 | 8.9 | air | Y | Y | Y | Y | 186 | 8 |
| **Rodentia** | | | | | | | | | | |
| *?* | Lemming | 0.045 | 0.40 | air | Y | Y | Y | Y | 230 | |
| | | 0.052 | 0.62 | air | Y | Y | Y | Y | 230 | |
| | | 0.056 | 0.54 | air | Y | Y | Y | Y | 230 | |
| *Acomys cahirinus* | Cairo spiny mouse | 0.042 | 5.3 | air | Y | Y | Y | Y | 234 | 8 |
| *Acomys russatus* | Golden spiny mouse | 0.056 | 5.0 | air | Y | Y | Y | Y | 234 | 8 |
| *Acomys spinosissimus* | Southern African spiny mouse | 0.027 | 5.1 | air | Y | Y | Y | Y | 209 | 8 |
| *Acomys subspinosus* | Cape spiny mouse | 0.032 | 9.7 | air | Y | Y | Y | Y | 209 | 8 |
| *Aconaemys fuscus* | Chilean rock rat | 0.11 | 14.0 | air | Y | Y | Y | Y | 179 | 8 |
| *Aethomys namaquensis* | Namaqua rock rat | 0.064 | 6.6 | air | Y | Y | Y | Y | 157 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Agouti paca* | Lowland paca | 4.5 | 229.6 | air | Y | Y | Y | Y | 178 | |
| | | 9.2 | 318.0 | air | Y | Y | Y | Y | 2 | 8 |
| *Akodon albiventer* | White-bellied grass mouse | 0.031 | 5.4 | air | Y | Y | Y | Y | 20 | 8 |
| *Akodon azarae* | Azara's grass mouse | 0.024 | 4.7 | air | Y | Y | Y | Y | 22 | 8 |
| *Akodon lanosus* | Woolly grass mouse | 0.024 | 5.3 | air | Y | Y | Y | Y | 20 | 8 |
| *Akodon longipilis* | Long-haired grass mouse | 0.042 | 6.7 | air | Y | Y | Y | Y | 22 | 8 |
| *Akodon olivaceus* | Olive grass mouse | 0.027 | 5.7 | air | Y | Y | Y | Y | 22 | 8 |
| *Alticola argentatus* | Silver mountain vole | 0.038 | 14.0 | air | Y | Y | Y | Y | 259 | 8 |
| *Alticola roylei* | Royle's mountain vole | 0.053 | 14.1 | air | Y | Y | Y | Y | 259 | 4 |
| *Ammospermophilus leucurus* | White-tailed antelope squirrel | 0.096 | 10.9 | air | Y | Y | Y | Y | | 8 |
| *Aplodontia rufa* | Mountain beaver | 0.63 | 32.1 | air | Y | Y | Y | Y | 174 | 8 |
| *Apodemus flavicollis* | Yellow-necked mouse | 0.024 | 5.0 | air | Y | Y | Y | Y | 94 | 8 |
| *Apodemus hermonensis* | Steppe field mouse | 0.020 | 5.8 | air | Y | Y | Y | Y | 94 | 8 |
| *Apodemus mystacinus* | Broad-toothed field mouse | 0.040 | 6.5 | air | Y | Y | Y | Y | 93 | 8 |
| *Apodemus sylvaticus* | Wood mouse | 0.024 | 5.0 | air | Y | Y | Y | Y | 93 | 8 |
| *Arborimus longicaudus* | Red tree vole | 0.022 | 6.8 | air | Y | Y | Y | Y | 180 | 8 |
| *Arvicola richardsoni* | Water vole | 0.051 | 10.3 | air | Y | Y | Y | Y | 178 | 4 |
| *Arvicola terrestris* | European water vole | 0.092 | 12.4 | air | Y | Y | Y | Y | 180 | 8 |
| | | 0.097 | 13.0 | air | Y | Y | Y | Y | 66 | 4 |
| *Auliscomys boliviensis* | Bolivian big-eared mouse | 0.077 | 12.8 | air | Y | Y | Y | Y | 22 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Auliscomys micropus* | Southern big-eared mouse | 0.062 | 11.3 | air | Y | Y | Y | Y | 22 | 8 |
| *Baiomys taylori* | Northern pygmy mouse | 0.007 | 2.0 | air | Y | Y | Y | Y | 156 | 8 |
| *Bathyergus janetta* | Namaqua dune mole rat | 0.406 | 24.9 | air | Y | Y | Y | Y | 154 | 8 |
| *Bathyergus suillus* | Cape dune mole rat | 0.62 | 35.2 | air | Y | Y | Y | Y | 154 | 8 |
| *Calomys musculinus* | Drylands vesper mouse | 0.017 | 3.2 | air | Y | Y | Y | Y | 22 | 8 |
| *Cannomys badius* | Lesser bamboo rat | 0.34 | 19.9 | air | Y | Y | Y | Y | 174 | 8 |
| *Capromys pilorides* | Desmarest's hutia | 2.6 | 70.0 | air | Y | Y | Y | Y | 2 | 8 |
| *Cavia porcellus* | Guinea pig | 0.629 | 40.1 | air | Y | Y | Y | Y | 2 | 8 |
| *Chaetodipus baileyi* | Bailey's pocket mouse | 0.029 | 4.0 | air | Y | Y | Y | Y | 115 | 8 |
| *Chaetodipus californicus* | California pocket mouse | 0.022 | 2.5 | air | Y | Y | Y | Y | 251 | 8 |
| *Chaetodipus fallax* | San Diego pocket mouse | 0.020 | 3.1 | air | Y | Y | Y | Y | 115 | 8 |
| *Chaetodipus hispidus* | Hispid pocket mouse | 0.040 | 5.7 | air | Y | Y | Y | Y | 255 | 8 |
| *Chaetodipus intermedius* | Rock pocket mouse | 0.015 | 2.1 | air | Y | Y | Y | Y | 24 | 8 |
| *Chaetodipus penicillatus* | Desert pocket mouse | 0.016 | 2.6 | air | Y | Y | Y | Y | 29 | 8 |
| *Chelemys macronyx* | Andean long-clawed mouse | 0.062 | 9.8 | air | Y | Y | Y | Y | 22 | 8 |
| *Chinchilla lanigera* | Long-tailed chinchilla | 0.40 | 32.7 | air | Y | Y | Y | Y | 65 | 4 |
| | | 0.43 | 23.2 | air | Y | Y | Y | Y | 2 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Chionomys nivalis* | European snow vole | 0.033 | 9.4 | air | Y | Y | Y | Y | 156 | 8 |
| *Chroeomys andinus* | Andean altiplano mouse | 0.035 | 7.5 | air | Y | Y | Y | Y | 22 | 8 |
| *Clethrionomys californicus* | Western red-backed vole | 0.018 | 7.1 | air | Y | Y | Y | Y | 180 | 8 |
| *Clethrionomys gapperi* | Southern red-backed vole | 0.022 | 5.7 | air | Y | Y | Y | Y | 180 | 8 |
| *Clethrionomys glareolus* | Bank vole | 0.023 | 7.3 | air | Y | Y | Y | Y | 156 | 8 |
| *Clethrionomys rufocanus* | Grey red-backed vole | 0.027 | 6.9 | air | Y | Y | Y | Y | 180 | 8 |
| *Clethrionomys rutilus* | Northern red-backed vole | 0.028 | 8.9 | air | Y | Y | Y | Y | 223 | 8 |
| *Coendou prehensilis* | Brazilian porcupine | 3.3 | 106.3 | air | Y | Y | Y | Y | 2 | 8 |
| *Conilurus penicillatus* | Brush-tailed rabbit rat | 0.21 | 18.8 | air | Y | Y | Y | Y | 116 | 8 |
| *Cricetomys gambianus* | Gambian pouched rat | 1.9 | 132.1 | air | Y | Y | Y | Y | 138 | 8 |
| *Cricetulus migratorius* | Gray dwarf hamster | 0.031 | 5.1 | air | Y | Y | Y | Y | 93 | 8 |
| *Cricetus cricetus* | European hamster | 0.36 | 26.8 | air | Y | Y | Y | Y | 102 | 8 |
| *Cryptomys bocagei* | Bocage's mole rat | 0.094 | 8.1 | air | Y | Y | Y | Y | 10 | 8 |
| *Cryptomys damarensis* | Damaraland mole rat | 0.14 | 9.1 | air | Y | Y | Y | Y | 154 | 8 |
| *Cryptomys hottentotus* | Common mole rat | 0.079 | 7.6 | air | Y | Y | Y | Y | 11 | 8 |
| *Cryptomys mechowi* | Mechow's mole rat | 0.27 | 18.5 | air | Y | Y | Y | Y | 10 | 8 |
| *Ctenomys australis* | Southern tuco-tuco | 0.34 | 13.5 | air | Y | Y | Y | Y | 33 | 8 |
| *Ctenomys fulvus* | Tawny tuco-tuco | 0.30 | 21.9 | air | Y | Y | Y | Y | 179 | 8 |
| *Ctenomys maulinus* | Maule tuco-tuco | 0.22 | 21.7 | air | Y | Y | Y | Y | 2 | 8 |

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|---|---|---|---|---|---|---|---|---|---|
| *Ctenomys opimus* | Highland tuco-tuco | 0.21 | 12.7 | air | Y | Y | Y | Y | 2 | 8 |
| *Ctenomys peruanus* | Peruvian tuco-tuco | 0.49 | 25.5 | air | Y | Y | Y | Y | 2 | 8 |
| *Ctenomys talarum* | Talas tuco-tuco | 0.12 | 12.7 | air | Y | Y | Y | Y | 33 | 8 |
| *Cynomys ludovicianus* | Black-tailed prairie dog | 1.1 | 48.9 | air | Y | Y | Y | Y | 212 | 8 |
| *Dasyprocta azarae* | Azara's agouti | 3.8 | 218.4 | air | Y | Y | Y | Y | 2 | 8 |
| *Dasyprocta leporina* | Red-rumped agouti | 2.7 | 180.4 | air | Y | Y | Y | Y | 2 | 8 |
| *Desmodillus auricularis* | Cape short-eared gerbil | 0.072 | 10.2 | air | Y | Y | Y | Y | 62 | 8 |
| *Dicrostonyx groenlandicus* | Northern collared lemming | 0.060 | 11.4 | air | Y | Y | Y | Y | 180 | 8 |
| *Dicrostonyx torquatus* | Arctic lemming | 0.047 | 10.7 | air | Y | Y | Y | Y | 37 | 4 |
| *Dipodomys agilis* | Agile kangaroo rat | 0.061 | 7.4 | air | Y | Y | Y | Y | 35 | 8 |
| *Dipodomys deserti* | Desert kangaroo rat | 0.106 | 10.7 | air | Y | Y | Y | Y | 2 | 8 |
| *Dipodomys heermanni* | Heermann's kangaroo rat | 0.063 | 8.5 | air | Y | Y | Y | Y | 116 | 8 |
| *Dipodomys merriami* | Merriam's kangaroo rat | 0.036 | 4.9 | air | Y | Y | Y | Y | 59 | 8 |
| *Dipodomys microps* | Chisel-toothed kangaroo rat | 0.057 | 7.7 | air | Y | Y | Y | Y | 26 | 8 |
| *Dipodomys nitratoides* | Fresno kangaroo rat | 0.038 | 5.3 | air | Y | Y | Y | Y | 116 | 8 |
| *Dipodomys ordii* | Ord's kangaroo rat | 0.047 | 7.4 | air | Y | Y | Y | Y | 115 | 8 |
| *Dipodomys panamintinus* | Panamint kangaroo rat | 0.064 | 8.6 | air | Y | Y | Y | Y | 102 | 8 |
| *Dipus sagitta* | Northern three-toed jerboa | 0.16 | 14.0 | air | Y | Y | Y | Y | 102 | 8 |
| *Dolichotis salinicola* | Chacoan mara | 1.6 | 84.0 | air | Y | Y | Y | Y | 2 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Eligmodontia typus* | Highland gerbil mouse | 0.018 | 3.5 | air | Y | Y | Y | Y | 22 | 8 |
| *Epixerus wilsoni* | Wilson's squirrel | 0.46 | 28.0 | air | Y | Y | Y | Y | 156 | 8 |
| *Erethizon dorsatum* | North American porcupine | 11.1 | 322.3 | air | Y | Y | Y | Y | 2 | 8 |
| *Euneomys chinchilloides* | Patagonian chinchilla mouse | 0.065 | 9.8 | air | Y | Y | Y | Y | 20 | 8 |
| *Funisciurus congicus* | Congo rope squirrel | 0.11 | 11.1 | air | Y | Y | Y | Y | 252 | 8 |
| *Funisciurus isabella* | Lady Burton's rope squirrel | 0.060 | 11.8 | air | Y | Y | Y | Y | 156 | 8 |
| *Funisciurus lemniscatus* | Ribboned rope squirrel | 0.095 | 10.4 | air | Y | Y | Y | Y | 156 | 8 |
| *Funisciurus pyrropus* | Fire-footed rope squirrel | 0.24 | 21.0 | air | Y | Y | Y | Y | 156 | 8 |
| *Galea musteloides* | Common yellow-toothed cavy | 0.32 | 30.6 | air | Y | Y | Y | Y | 2 | 8 |
| *Geocapromys brownii* | Jamaican coney | 2.5 | 85.3 | air | Y | Y | Y | Y | 2 | 8 |
| *Geocapromys ingrahami* | Bahamian hutia | 0.78 | 30.8 | air | Y | Y | Y | Y | 2 | 8 |
| *Geomys bursarius* | Plains pocket gopher | 0.20 | 16.0 | air | Y | Y | Y | Y | 25 | 8 |
| *Geomys pinetis* | Southeastern pocket gopher | 0.17 | 15.4 | air | Y | Y | Y | Y | 170 | 8 |
| *Georychus capensis* | Cape mole rat | 0.19 | 13.4 | air | Y | Y | Y | Y | 68 | 8 |
| *Gerbillurus paeba* | Hairy-footed gerbil | 0.034 | 4.0 | air | Y | Y | Y | Y | 61 | 8 |
| *Gerbillurus setzeri* | Namib brush-tailed gerbil | 0.046 | 4.3 | air | Y | Y | Y | Y | 61 | 8 |
| *Gerbillurus tytonis* | Dune hairy-footed gerbil | 0.030 | 3.7 | air | Y | Y | Y | Y | 61 | 8 |

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|---|---|---|---|---|---|---|---|---|---|
| *Gerbillurus vallinus* | Bushy-tailed hairy-footed gerbil | 0.039 | 4.0 | air | Y | Y | Y | Y | 61 | 8 |
| *Gerbillus allenbyi* | Anderson's gerbil | 0.035 | 4.5 | air | Y | Y | Y | Y | 89 | 8 |
| *Gerbillus dasyurus* | Wagner's gerbil | 0.028 | 3.4 | air | Y | Y | Y | Y | 90 | 8 |
| *Gerbillus gerbillus* | Lesser gerbil | 0.030 | 4.9 | air | Y | Y | Y | Y | 93 | 8 |
| *Gerbillus nanus* | Balochistan gerbil | 0.028 | 2.6 | air | Y | Y | Y | Y | 93 | 8 |
| *Gerbillus perpallidus* | Pale gerbil | 0.052 | 5.0 | air | Y | Y | Y | Y | 156 | 8 |
| *Gerbillus pusillus* | Least gerbil | 0.013 | 1.6 | air | Y | Y | Y | Y | 32 | 8 |
| *Gerbillus pyramidum* | Greater Egyptian gerbil | 0.11 | 9.4 | air | Y | Y | Y | Y | 218 | 8 |
| *Glaucomys volans* | Southern flying squirrel | 0.064 | 7.8 | air | Y | Y | Y | Y | 241 | 8 |
| | | 0.070 | 10.5 | air | Y | Y | Y | Y | 198 | 4 |
| *Golunda ellioti* | Indian bush rat | 0.056 | 7.0 | air | Y | Y | Y | Y | 87 | 4 |
| *Graomys griseoflavus* | Gray leaf-eared mouse | 0.069 | 9.7 | air | Y | Y | Y | Y | 22 | 8 |
| *Graphiurus ocularis* | Spectacled dormouse | 0.068 | 7.7 | air | Y | Y | Y | Y | 156 | 8 |
| *Heliophobius argenteocinereus* | Silvery mole rat | 0.088 | 8.7 | air | Y | Y | Y | Y | 174 | 8 |
| *Heliosciurus rufobrachium* | Red-legged sun squirrel | 0.23 | 15.4 | air | Y | Y | Y | Y | 156 | 8 |
| *Heterocephalus glaber* | Naked mole rat | 0.032 | 2.4 | air | Y | Y | Y | Y | 170 | 8 |
| *Heteromys anomalus* | Trinidad spiny pocket mouse | 0.069 | 11.6 | air | Y | Y | Y | Y | 2 | 8 |
| *Heteromys desmarestianus* | Desmarest's spiny pocket mouse | 0.076 | 11.5 | air | Y | Y | Y | Y | 115 | 8 |

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|---|---|---|---|---|---|---|---|---|---|
| *Hydrochaeris hydrochaeris* | Capybara | 26.4 | 763.7 | air | Y | Y | Y | Y | 2 | 8 |
| *Hydromys chrysogaster* | Rakali | 0.90 | 61.2 | air | Y | Y | Y | Y | 58 | 8 |
| *Hystrix africaeaustralis* | Cape porcupine | 11.3 | 273.4 | air | Y | Y | Y | Y | 2 | 8 |
| *Isthmomys pirrensis* | Mount Pirri isthmus rat | 0.14 | 14.0 | air | Y | Y | Y | Y | 111 | 8 |
| *Jaculus jaculus* | Lesser Egyptian jerboa | 0.075 | 10.7 | air | Y | Y | Y | Y | 118 | 8 |
| *Jaculus orientalis* | Greater Egyptian jerboa | 0.14 | 16.1 | air | Y | Y | Y | Y | 118 | 8 |
| *Kerodon rupestris* | Rocky cavy | 0.80 | 41.7 | air | Y | Y | Y | Y | 2 | 8 |
| *Lagostomus maximus* | Plains viscacha | 6.8 | 219.9 | air | Y | Y | Y | Y | 2 | 8 |
| *Lagurus curtatus* | Sagebrush vole | 0.029 | 5.2 | air | Y | Y | Y | Y | 178 | 4 |
| *Lagurus lagurus* | Steppe lemming | 0.030 | 5.8 | air | Y | Y | Y | Y | 180 | 8 |
| *Lemmus lemmus* | Norway lemming | 0.080 | 22.2 | air | Y | Y | Y | Y | 117 | 8 |
| *Lemmus sibericus* | Siberian brown lemming | 0.064 | 18.3 | air | Y | Y | Y | Y | 37 | 4 |
| | | 0.050 | 10.4 | air | Y | Y | Y | Y | 180 | 8 |
| *Lemniscomys griselda* | Griselda's striped grass mouse | 0.048 | 6.7 | air | Y | Y | Y | Y | 90 | 8 |
| | | 0.051 | 7.1 | air | Y | Y | Y | Y | 88 | 4 |
| *Lemniscomys rosalia* | Single-striped grass mouse | 0.051 | 7.1 | air | Y | Y | Y | Y | 88 | 8 |
| *Liomys irroratus* | Mexican spiny pocket mouse | 0.048 | 6.2 | air | Y | Y | Y | Y | 123 | 8 |
| *Liomys salvini* | Salvin's spiny pocket mouse | 0.044 | 5.4 | air | Y | Y | Y | Y | 123 | 8 |
| *Malacothrix typica* | Gerbil mouse | 0.022 | 2.4 | air | Y | Y | Y | Y | 139 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Marmota flaviventris* | Yellow-bellied marmot | 4.3 | 179.0 | air | Y | Y | Y | Y | 212 | 8 |
| *Marmota monax* | Groundhog | 2.7 | 76.7 | air | Y | Y | Y | Y | 9 | 8 |
| *Mastomys natalensis* | Natal multimammate mouse | 0.042 | 3.8 | air | Y | Y | Y | Y | 92 | 8 |
| *Megadontomys thomasi* | Thomas's giant deer mouse | 0.11 | 14.4 | air | Y | Y | Y | Y | 102 | 8 |
| *Meriones hurrianae* | Indian desert jird | 0.069 | 6.3 | air | Y | Y | Y | Y | 87 | 8 |
| *Meriones tristrami* | Tristram's jird | 0.11 | 11.4 | air | Y | Y | Y | Y | 93 | 8 |
| *Meriones unguiculatus* | Mongolian gerbil | 0.067 | 8.9 | air | Y | Y | Y | Y | 259 | 8 |
| *Mesocricetus auratus* | Golden hamster | 0.098 | 17.0 | air | Y | Y | Y | Y | 102 | 8 |
| *Microcavia niata* | Andean mountain cavy | 0.25 | 20.3 | air | Y | Y | Y | Y | 156 | 8 |
| *Microdipodops megacephalus* | Dark kangaroo mouse | 0.011 | 3.5 | air | Y | Y | Y | Y | 115 | 8 |
| *Microdipodops pallidus* | Pale kangaroo mouse | 0.015 | 2.3 | air | Y | Y | Y | Y | 4 | 8 |
| *Micromys minutus* | Eurasian harvest mouse | 0.007 | 2.4 | air | Y | Y | Y | Y | 102 | 8 |
| *Microtus agrestis* | Field vole | 0.022 | 7.6 | air | Y | Y | Y | Y | 100 | 4 |
| | | 0.028 | 7.4 | air | Y | Y | Y | Y | 167 | 8 |
| *Microtus arvalis* | Common vole | 0.020 | 7.2 | air | Y | Y | Y | Y | 128 | 8 |
| *Microtus breweri* | Beach vole | 0.053 | 8.5 | air | Y | Y | Y | Y | 147 | 8 |
| *Microtus californicus* | California vole | 0.044 | 7.9 | air | Y | Y | Y | Y | 180 | 8 |
| *Microtus guentheri* | Gunther's vole | 0.044 | 9.3 | air | Y | Y | Y | Y | 93 | 8 |
| *Microtus longicaudus* | Long-tailed vole | 0.027 | 8.3 | air | Y | Y | Y | Y | 7 | 4 |
| | | 0.029 | 7.8 | air | Y | Y | Y | Y | 180 | 8 |

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|---|---|---|---|---|---|---|---|---|---|
| *Microtus mexicanus* | Mexican vole | 0.029 | 5.4 | air | Y | Y | Y | Y | 180 | 8 |
| *Microtus montanus* | Montane vole | 0.031 | 9.5 | air | Y | Y | Y | Y | 206 | 4 |
| | | 0.035 | 9.6 | air | Y | Y | Y | Y | 180 | 8 |
| *Microtus nivalis* | European snow vole | 0.035 | 12.4 | air | Y | Y | Y | Y | 13 | 4 |
| *Microtus ochrogaster* | Prairie vole | 0.047 | 9.2 | air | Y | Y | Y | Y | 180 | 8 |
| | | 0.051 | 7.0 | air | Y | Y | Y | Y | 178 | |
| *Microtus oeconomus* | Tundra vole | 0.032 | 9.3 | air | Y | Y | Y | Y | 37 | 4 |
| | | 0.034 | 11.7 | air | Y | Y | Y | Y | 180 | 8 |
| *Microtus pennsylvanicus* | Meadow vole | 0.039 | 8.7 | air | Y | Y | Y | Y | 180 | 8 |
| *Microtus pinetorum* | Woodland vole | 0.025 | 6.8 | air | Y | Y | Y | Y | 180 | 8 |
| *Microtus richardsoni* | Water vole | 0.066 | 14.8 | air | Y | Y | Y | Y | 180 | 8 |
| *Microtus subterraneus* | European pine vole | 0.018 | 5.7 | air | Y | Y | Y | Y | 156 | 8 |
| *Microtus townsendii* | Townsend's vole | 0.052 | 10.5 | air | Y | Y | Y | Y | 137 | 8 |
| *Microtus xanthognathus* | Taiga vole | 0.068 | 11.4 | air | Y | Y | Y | Y | 180 | 8 |
| *Millardia meltada* | Soft-furred rat | 0.067 | 6.8 | air | Y | Y | Y | Y | 156 | 8 |
| *Mus minutoides* | African pygmy mouse | 0.008 | 2.8 | air | Y | Y | Y | Y | 64 | 8 |
| *Mus spretus* | Algerian mouse | 0.022 | 7.2 | air | Y | Y | Y | Y | 156 | 8 |
| *Muscardinus avellanarius* | Hazel dormouse | 0.023 | 7.3 | air | Y | Y | Y | Y | 80 | 8 |
| *Myocaster coypus* | Coypu | 4.3 | 350.5 | air | Y | Y | Y | Y | 232 | 4 |
| *Myoprocta acouchy* | Red acouchi | 0.91 | 58.2 | air | Y | Y | Y | Y | 2 | 8 |
| *Myopus schisticolor* | Wood lemming | 0.026 | 10.8 | air | Y | Y | Y | Y | 227 | 8 |
| *Myoxus glis* | Edible dormouse | 0.20 | 18.3 | air | Y | Y | Y | Y | 80 | 8 |
| *Mystromys albicaudatus* | White-tailed rat | 0.094 | 14.7 | air | Y | Y | Y | Y | 63 | 8 |
| *Nannospalax ehrenbergi* | Middle East Blind mole rat | 0.14 | 12.1 | air | Y | Y | Y | Y | 201 | 8 |
| *Nannospalax leucodon* | Lesser mole rat | 0.20 | 17.2 | air | Y | Y | Y | Y | 174 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Napaeozapus insignis* | Woodland jumping mouse | 0.022 | 4.6 | air | Y | Y | Y | Y | 29 | 8 |
| *Neofiber alleni* | Round-tailed muskrat | 0.26 | 25.1 | air | Y | Y | Y | Y | 180 | 8 |
| *Neotoma cinerea* | Bushy-tailed woodrat | 0.21 | 19.5 | air | Y | Y | Y | Y | 178 | 8 |
| *Neotoma fuscipes* | Dusky-footed woodrat | 0.19 | 17.1 | air | Y | Y | Y | Y | 172 | 8 |
| *Neotoma labigula* | White-throated woodrat | 0.18 | 15.6 | air | Y | Y | Y | Y | 178 | 8 |
| | | 0.19 | 16.4 | air | Y | Y | Y | Y | 30 | 4 |
| *Neotoma lepida* | Desert woodrat | 0.11 | 10.1 | air | Y | Y | Y | Y | 172 | 8 |
| *Notomys alexis* | Spinifex hopping mouse | 0.032 | 5.2 | air | Y | Y | Y | Y | 161 | 8 |
| *Notomys cervinus* | Fawn hopping mouse | 0.034 | 4.8 | air | Y | Y | Y | Y | 161 | 8 |
| *Ochrotomys nuttalli* | Golden mouse | 0.019 | 3.1 | air | Y | Y | Y | Y | 149 | 8 |
| *Octodon bridgesi* | Bridges' degu | 0.18 | 21.2 | air | Y | Y | Y | Y | 20 | 8 |
| *Octodon degus* | Degu | 0.19 | 19.7 | air | Y | Y | Y | Y | 2 | 8 |
| *Octodon lunatus* | Moon-toothed degu | 0.17 | 19.9 | air | Y | Y | Y | Y | 20 | 8 |
| *Octodontomys gliroides* | Mountain degu | 0.15 | 15.1 | air | Y | Y | Y | Y | 2 | 8 |
| *Octomys mimax* | Viscacha rat | 0.12 | 13.3 | air | Y | Y | Y | Y | 21 | 8 |
| *Oligoryzomys longicaudatus* | Long-tailed pygmy rice rat | 0.028 | 5.9 | air | Y | Y | Y | Y | 22 | 8 |
| *Ondatra zibethicus* | Muskrat | 0.84 | 79.9 | air | Y | Y | Y | Y | 233 | 4 |
| | | 1.0 | 74.4 | air | Y | Y | Y | Y | 180 | 8 |
| *Onychomys torridus* | Southern grasshopper mouse | 0.019 | 3.4 | air | Y | Y | Y | Y | 263 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Otomys irroratus* | Southern African vlei rat | 0.10 | 9.8 | air | Y | Y | Y | Y | 90 | 8 |
| *Otomys sloggetti* | Sloggett's vlei rat | 0.11 | 15.5 | air | Y | Y | Y | Y | 215 | 8 |
| *Otomys unisulcatus* | Bush vlei rat | 0.096 | 12.3 | air | Y | Y | Y | Y | 67 | 8 |
| *Oxymycterus roberti* | Robert's hocicudo | 0.083 | 10.5 | air | Y | Y | Y | Y | 177 | 8 |
| *Paraxerus cepapi* | Smith's bush squirrel | 0.22 | 16.8 | air | Y | Y | Y | Y | 177 | 8 |
| *Paraxerus palliatus* | Red bush squirrel | 0.29 | 25.2 | air | Y | Y | Y | Y | 252 | 8 |
| *Parotomys brantsii* | Brants's whistling rat | 0.086 | 9.7 | air | Y | Y | Y | Y | 67 | 8 |
| *Pedetes capensis* | South African springhare | 2.3 | 91.9 | air | Y | Y | Y | Y | 156 | 8 |
| *Perognathus flavus* | Silky pocket mouse | 0.008 | 2.0 | air | Y | Y | Y | Y | 115 | 8 |
| *Perognathus longimembris* | Little pocket mouse | 0.009 | 1.1 | air | Y | Y | Y | Y | 44 | 8 |
| *Peromyscus boylii* | Brush mouse | 0.023 | 6.3 | air | Y | Y | Y | Y | 165 | 8 |
| *Peromyscus californicus* | California mouse | 0.048 | 6.0 | air | Y | Y | Y | Y | 185 | 8 |
| *Peromyscus crinitus* | Canyon mouse | 0.016 | 2.9 | air | Y | Y | Y | Y | 185 | 8 |
| *Peromyscus eremicus* | Cactus mouse | 0.022 | 3.8 | air | Y | Y | Y | Y | 185 | 8 |
| *Peromyscus gossypinus* | Cotton mouse | 0.022 | 4.3 | air | Y | Y | Y | Y | 84 | 8 |
| *Peromyscus leucopus* | White-footed mouse | 0.023 | 5.2 | air | Y | Y | Y | Y | 80 | 8 |
| *Peromyscus maniculatus* | Deer mouse | 0.021 | 4.6 | air | Y | Y | Y | Y | 185 | 8 |
| *Peromyscus megalops* | Brown deer mouse | 0.066 | 10.5 | air | Y | Y | Y | Y | 179 | 8 |
| *Peromyscus oreas* | Northwestern deer mouse | 0.025 | 5.0 | air | Y | Y | Y | Y | 104 | 8 |
| *Peromyscus polionotus* | Oldfield mouse | 0.012 | 2.5 | air | Y | Y | Y | Y | 84 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Peromyscus sitkensis* | Northwestern deer mouse | 0.028 | 5.4 | air | Y | Y | Y | Y | 104 | 8 |
| *Peromyscus truei* | Pinyon mouse | 0.033 | 6.6 | air | Y | Y | Y | Y | 185 | 8 |
| *Phenacomys intermedius* | Western heather vole | 0.022 | 7.8 | air | Y | Y | Y | Y | 180 | 8 |
| | | 0.026 | 9.0 | air | Y | Y | Y | Y | 178 | 4 |
| *Phodopus sungorus* | Djungarian hamster | 0.026 | 4.7 | air | Y | Y | Y | Y | 260 | 8 |
| *Phyllotis darwini* | Darwin's leaf-eared mouse | 0.048 | 7.0 | air | Y | Y | Y | Y | 22 | 8 |
| *Phyllotis magister* | Master leaf-eared mouse | 0.063 | 8.0 | air | Y | Y | Y | Y | 214 | 8 |
| *Phyllotis xanthopygus* | Yellow-rumped leaf-eared mouse | 0.055 | 6.6 | air | Y | Y | Y | Y | 22 | 8 |
| *Pitymys pinetorum* | Woodland vole | 0.025 | 5.7 | air | Y | Y | Y | Y | 178 | 4 |
| *Podomys floridanus* | Florida mouse | 0.031 | 6.0 | air | Y | Y | Y | Y | 84 | 8 |
| *Proechimys semispinosus* | Tome's spiny rat | 0.50 | 36.3 | air | Y | Y | Y | Y | 2 | 8 |
| *Pseudomys gracilicaudatus* | Eastern chestnut mouse | 0.080 | 9.7 | air | Y | Y | Y | Y | 57 | 8 |
| *Pseudomys hermannsburgensis* | Sandy inland mouse | 0.012 | 2.7 | air | Y | Y | Y | Y | 160 | 8 |
| *Rattus colletti* | Dusky rat | 0.17 | 14.2 | air | Y | Y | Y | Y | 116 | 8 |
| *Rattus fuscipes* | Bush rat | 0.076 | 9.8 | air | Y | Y | Y | Y | 46 | 8 |
| *Rattus lutreolus* | Australian swamp rat | 0.11 | 7.3 | air | Y | Y | Y | Y | 47 | 8 |
| *Rattus sordidus* | Dusky field rat | 0.19 | 12.3 | air | Y | Y | Y | Y | 48 | 8 |
| *Rattus villosissimus* | Long-haired rat | 0.25 | 16.9 | air | Y | Y | Y | Y | 116 | 8 |
| *Reithrodon auritus* | Bunny rat | 0.079 | 8.9 | air | Y | Y | Y | Y | 20 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Reithrodontomys megalotis* | Western harvest mouse | 0.009 | 2.6 | air | Y | Y | Y | Y | 208 | 8 |
| *Rhabdomys pumilio* | Four-striped grass mouse | 0.040 | 3.7 | air | Y | Y | Y | Y | 90 | 8 |
| *Saccostomus campestris* | South African pouched mouse | 0.061 | 6.0 | air | Y | Y | Y | Y | 95 | 8 |
| *Sciurus aberti* | Abert's squirrel | 0.62 | 49.8 | air | Y | Y | Y | Y | 85 | 8 |
| *Sciurus carolinensis* | Eastern gray squirrel | 0.44 | 42.8 | air | Y | Y | Y | Y | 16 | 8 |
| *Scotinomys teguina* | Alston's brown mouse | 0.012 | 3.6 | air | Y | Y | Y | Y | 112 | 8 |
| *Scotinomys xerampelinus* | Chiriqui brown mouse | 0.015 | 3.7 | air | Y | Y | Y | Y | 112 | 8 |
| *Sekeetamys calurus* | Bushy-tailed jird | 0.057 | 5.1 | air | Y | Y | Y | Y | 91 | 8 |
| *Sicista betulina* | Northern birch mouse | 0.010 | 3.7 | air | Y | Y | Y | Y | 156 | 8 |
| *Sigmodon alleni* | Allen's cotton rat | 0.14 | 23.5 | air | Y | Y | Y | Y | 18 | 8 |
| *Sigmodon fulviventer* | Tawny-bellied cotton rat | 0.14 | 24.0 | air | Y | Y | Y | Y | 18 | 8 |
| *Sigmodon hispidus* | Hispid cotton rat | 0.14 | 26.7 | air | Y | Y | Y | Y | 18 | 8 |
| | | 0.14 | 16.8 | air | Y | Y | Y | Y | 18 | 8 |
| *Sigmodon leucotis* | White-eared cotton rat | 0.13 | 21.6 | air | Y | Y | Y | Y | 18 | 8 |
| *Sigmodon ochrognathus* | Yellow-nosed cotton rat | 0.12 | 17.9 | air | Y | Y | Y | Y | 18 | 8 |
| *Spalacopus cyanus* | Cururo | 0.14 | 12.4 | air | Y | Y | Y | Y | 174 | 8 |
| *Spermophilus armatus* | Uinta ground squirrel | 0.32 | 17.0 | air | Y | Y | Y | Y | 122 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Spermophilus beecheyi* | California ground squirrel | 0.60 | 36.8 | air | Y | Y | Y | Y | 5 | 8 |
| *Spermophilus beldingi* | Belding's ground squirrel | 0.30 | 14.7 | air | Y | Y | Y | Y | 122 | 8 |
| *Spermophilus citellus* | European ground squirrel | 0.24 | 26.4 | air | Y | Y | Y | Y | 102 | 8 |
| *Spermophilus lateralis* | Golden-mantled ground squirrel | 0.24 | 16.6 | air | Y | Y | Y | Y | 122 | 8 |
| *Spermophilus mohavensis* | Mohave ground squirrel | 0.24 | 13.1 | air | Y | Y | Y | Y | 122 | 8 |
| *Spermophilus parryii* | Arctic ground squirrel | 0.65 | 60.2 | air | Y | Y | Y | Y | 80 | 8 |
| *Spermophilus richardsonii* | Richardson's ground squirrel | 0.27 | 15.2 | air | Y | Y | Y | Y | 122 | 8 |
| *Spermophilus saturatus* | Cascade golden-mantled ground squirrel | 0.25 | 18.7 | air | Y | Y | Y | Y | 137 | 8 |
| *Spermophilus spilosoma* | Spotted ground squirrel | 0.17 | 10.7 | air | Y | Y | Y | Y | 122 | 8 |
| *Spermophilus tereticaudus* | Round-tailed ground squirrel | 0.17 | 10.8 | air | Y | Y | Y | Y | 122 | 8 |
| *Spermophilus townsendii* | Townsend's ground squirrel | 0.23 | 12.2 | air | Y | Y | Y | Y | 122 | 8 |
| *Spermophilus tridecemlineatus* | Thirteen-lined ground squirrel | 0.21 | 16.3 | air | Y | Y | Y | Y | 122 | 8 |
| *Spermophilus undulatus* | Long-tailed ground squirrel | 0.68 | 77.2 | air | Y | Y | Y | Y | 36 | 8 |

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|---|---|---|---|---|---|---|---|---|---|
| *Steatomys pratensis* | Fat mouse | 0.038 | 2.2 | air | Y | Y | Y | Y | 156 | 8 |
| *Stochomys longicaudatus* | Target rat | 0.084 | 11.3 | air | Y | Y | Y | Y | 156 | 8 |
| *Tachyoryctes splendens* | East African mole rat | 0.19 | 17.5 | air | Y | Y | Y | Y | 174 | 8 |
| *Tamias alpinus* | Alpine chipmunk | 0.039 | 6.7 | air | Y | Y | Y | Y | 178 | 8 |
| *Tamias amoenus* | Yellow-pine chipmunk | 0.057 | 11.1 | air | Y | Y | Y | Y | 131 | 8 |
| *Tamias merriami* | Merriam's chipmunk | 0.075 | 9.1 | air | Y | Y | Y | Y | 274 | 8 |
| *Tamias minimus* | Least chipmunk | 0.046 | 8.4 | air | Y | Y | Y | Y | 131 | 8 |
| *Tamias palmeri* | Palmer's chipmunk | 0.069 | 13.1 | air | Y | Y | Y | Y | 275 | 8 |
| *Tamias striatus* | Eastern chipmunk | 0.087 | 10.4 | air | Y | Y | Y | Y | 256 | 8 |
| *Tamiascirus hudsonicus* | American red squirrel | 0.11 | 15.5 | air | Y | Y | Y | Y | 200 | 4 |
| | | 0.22 | 28.3 | air | Y | Y | Y | Y | 207 | 4 |
| | | 0.22 | 33.4 | air | Y | Y | Y | Y | 207 | 8 |
| *Tatera afra* | Cape gerbil | 0.11 | 21.1 | air | Y | Y | Y | Y | 71 | 8 |
| *Tatera indica* | Indian gerbil | 0.087 | 8.8 | air | Y | Y | Y | Y | 87 | 8 |
| *Tatera leucogaster* | Bushveld gerbil | 0.16 | 15.3 | air | Y | Y | Y | Y | 62 | 8 |
| *Thallomys paedulcus* | Acacia rat | 0.13 | 10.1 | air | Y | Y | Y | Y | 157 | 8 |
| *Thomomys bottae* | Botta's pocket gopher | 0.14 | 13.9 | air | Y | Y | Y | Y | 253 | 8 |
| *Thomomys talpoides* | Northern pocket gopher | 0.11 | 16.4 | air | Y | Y | Y | Y | 24 | 8 |
| *Thomomys umbrinus* | Southern pocket gopher | 0.085 | 8.4 | air | Y | Y | Y | Y | 24 | 8 |
| *Thrichomys apereoides* | Common punare | 0.32 | 23.9 | air | Y | Y | Y | Y | 2 | 8 |
| *Tympanoctomys barrerae* | Plains viscacha rat | 0.071 | 8.9 | air | Y | Y | Y | Y | 21 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Uromys caudimaculatus* | Giant white-tailed rat | 0.81 | 66.1 | air | Y | Y | Y | Y | 116 | 8 |
| *Xerus inauris* | Cape ground squirrel | 0.54 | 37.8 | air | Y | Y | Y | Y | 96 | 8 |
| *Xerus princeps* | Mountain ground squirrel | 0.60 | 39.4 | air | Y | Y | Y | Y | 96 | 8 |
| *Zapus hudsonius* | Meadow jumping mouse | 0.024 | 4.1 | air | Y | Y | Y | Y | 80 | 8 |
| **Scandentia** | | | | | | | | | | |
| *Ptilocercus lowii* | Pen-tailed treeshrew | 0.058 | 5.0 | air | Y | Y | Y | Y | 264 | 8 |
| *Tupaia glis* | Common treeshrew | 0.12 | 10.8 | air | Y | Y | Y | Y | 23 | 8 |
| *Urogale everetti* | Mindanao treeshrew | 0.261 | 25.9 | air | Y | Y | Y | Y | 199 | 8 |
| **Soricomorpha** | | | | | | | | | | |
| *Amblysomus hottentotus* | Hottentot golden mole | 0.070 | 9.8 | air | Y | Y | Y | Y | 156 | 8 |
| *Blarina brevicauda* | Northern short-tailed shrew | 0.020 | 7.6 | air | Y | Y | Y | Y | 240 | 8 |
| *Blarina carolinensis* | Southern short-tailed shrew | 0.010 | 3.9 | air | Y | Y | Y | Y | 240 | 8 |
| *Condylura cristata* | Star-nosed mole | 0.049 | 12.8 | air | Y | Y | Y | Y | 34 | 8 |
| *Crocidura crossei* | Crosse's shrew | 0.010 | 2.6 | air | Y | Y | Y | Y | 239 | 8 |
| *Crocidura flavescens* | Greater red musk shrew | 0.033 | 5.2 | air | Y | Y | Y | Y | 156 | 8 |
| *Crocidura hildegardeae* | Hildegarde's shrew | 0.010 | 3.0 | air | Y | Y | Y | Y | 239 | 8 |
| *Crocidura leucodon* | Bicolored shrew | 0.012 | 3.5 | air | Y | Y | Y | Y | 156 | 8 |
| *Crocidura luna* | Moonshine shrew | 0.012 | 2.9 | air | Y | Y | Y | Y | 174 | 8 |

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|---|---|---|---|---|---|---|---|---|---|---|
| *Crocidura olivieri* | African giant shrew | 0.039 | 6.8 | air | Y | Y | Y | Y | 175 | 8 |
| *Crocidura poensis* | Fraser's musk shrew | 0.017 | 3.6 | air | Y | Y | Y | Y | 239 | 8 |
| *Crocidura russula* | Greater white-toothed shrew | 0.010 | 2.6 | air | Y | Y | Y | Y | 235 | 8 |
| *Crocidura russula* | Greater white-toothed shrew | 0.014 | 3.0 | air | Y | Y | Y | Y | 235 | 8 |
| *Crocidura suaveolens* | Lesser white-toothed shrew | 0.007 | 2.2 | air | Y | Y | Y | Y | 235 | 8 |
| *Crocidura viaria* | Savanna path shrew | 0.015 | 2.6 | air | Y | Y | Y | Y | 235 | 8 |
| *Cryptotis parva* | North American least shrew | 0.006 | 2.2 | air | Y | Y | Y | Y | 175 | 8 |
| *Neomys anomalus* | Mediterranean water shrew | 0.013 | 7.7 | air | Y | Y | Y | Y | 156 | 8 |
| *Neomys fodiens* | Eurasian water shrew | 0.014 | 7.7 | air | Y | Y | Y | Y | 240 | 8 |
| | | 0.017 | 6.3 | air | Y | Y | Y | Y | 240 | 8 |
| *Neurotrichus gibbsii* | American shrew mole | 0.012 | 5.4 | air | Y | Y | Y | Y | 155 | 8 |
| *Notiosorex crawfordi* | Crawford's gray shrew | 0.004 | 1.5 | air | Y | Y | Y | Y | 240 | 8 |
| *Scalopus aquaticus* | Eastern mole | 0.048 | 7.8 | air | Y | Y | Y | Y | 155 | 8 |
| *Scapanus latimanus* | Broad-footed mole | 0.061 | 8.8 | air | Y | Y | Y | Y | 174 | 8 |
| *Scapanus orarius* | Coast mole | 0.061 | 7.4 | air | Y | Y | Y | Y | 179 | 8 |
| *Scapanus townsendii* | Townsend's mole | 0.13 | 12.6 | air | Y | Y | Y | Y | 137 | 8 |
| *Sorex alpinus* | Alpine shrew | 0.008 | 5.6 | air | Y | Y | Y | Y | 239 | 8 |
| *Sorex araneus* | Common shrew | 0.008 | 7.0 | air | Y | Y | Y | Y | 156 | 8 |
| *Sorex cinereus* | Cinereus shrew | 0.003 | 3.6 | air | Y | Y | Y | Y | 240 | 8 |
| *Sorex coronatus* | Crowned shrew | 0.009 | 6.0 | air | Y | Y | Y | Y | 240 | 8 |

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|---|---|---|---|---|---|---|---|---|---|
| *Sorex minutus* | Eurasian pygmy shrew | 0.004 | 3.6 | air | Y | Y | Y | Y | 240 | 8 |
| *Sorex ornatus* | Ornate shrew | 0.010 | 6.1 | air | Y | Y | Y | Y | 156 | 8 |
| *Sorex vagrans* | Vagrant shrew | 0.005 | 3.3 | air | Y | Y | Y | Y | 240 | 8 |
| *Suncus etruscus* | Etruscan shrew | 0.002 | 1.7 | air | Y | Y | Y | Y | 132 | 8 |
| *Suncus murinus* | Asian house shrew | 0.030 | 6.9 | air | Y | Y | Y | Y | 205 | 8 |
| **Xenarthra** | | | | | | | | | | |
| *Bradypus varigatus* | Brown-throated sloth | 3.8 | 79.0 | air | Y | Y | Y | Y | 173 | 4 |
| *Choloepus hoffmanni* | Hoffmann's two-toed sloth | 4.2 | 93.5 | air | Y | Y | Y | Y | 173 | 4 |
| *Cyclopes didactylus* | Silky anteater | 0.24 | 13.3 | air | Y | Y | Y | Y | 177 | 8 |
| *Myrmecophaga tridactyla* | Giant anteater | 30.6 | 301.8 | air | Y | Y | Y | Y | 105 | 8 |
| *Tamandua mexicana* | Northern tamandua | 4.0 | 114.8 | air | Y | Y | Y | Y | 177 | 8 |
| *Tamandua tetradactyla* | Southern tamandua | 3.5 | 104.1 | air | Y | Y | Y | Y | 105 | 8 |

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# Appendices

## A.2.1 Field metabolic rates: eutherian mammals

Body mass (kg) and field metabolic rate (kcal $d^{-1}$) of eutherian mammals, with reference to original (Source 1) and review (Source 2) data sources. All data were used in comparisons labeled “All determinations” (Figs. 4.2A and 4.2C). Non-empirical data (estimates) and data collected from captive animals were excluded in comparisons labeled “Empirical determinations only” (Figs. 4.2B and 4.2D).

## Marine Mammals

| Scientific Name | Common Name | Mass (kg) | FMR (kcal d$^{-1}$) | Determination Type | Source (1) | Source (2) |
|---|---|---|---|---|---|---|
| **Carnivores** | | | | | | |
| **Mustelidae** | | | | | | |
| *Enhydra lutris* | Sea otter | 27.3 | 3749.9 | measurement | 99 | |
| **Mysticeti** | | | | | | |
| *Balaenoptera bonaerensis* | Minke whale | 7500.0 | 228603.5 | estimate | 78 | |
| *Balaenoptera borealis* | Sei whale | 17780.0 | 470898.4 | estimate | 78 | |
| *Balaenoptera musculus* | Blue whale | 84328.0 | 1793256.0 | estimate | 78 | |
| *Balaenoptera physalus* | Fin whale | 48000.0 | 128030.6 | estimate | 9 | 7 |
| *Balaenoptera physalus* | Fin whale | 48768.0 | 1120315.4 | estimate | 78 | |
| *Eubalaena australis* | Southern right whale | 55880.0 | 1259291.7 | estimate | 78 | |
| *Megaptera novaeangliae* | Humpback whale | 26924.0 | 672547.0 | estimate | 78 | |
| **Odobenidae** | | | | | | |
| *Odobenus rosmarus* | Walrus | 1310.0 | 91049.6 | measurement | 1 | |
| **Odontoceti** | | | | | | |
| *Orcinus orca* | Killer whale | 2800.0 | 163808.4 | estimate | 96 | |
| | | 3338.0 | 228216.0 | estimate | 69 | |
| | | 4434.0 | 184444.0 | estimate | 69 | |
| | | 4733.0 | 243605.9 | estimate | 96 | |
| **Otariidae** | | | | | | |
| *Arctocephalus galapagoensis* | Galapagos fur seal | 37.4 | 1144.0 | measurement | 20 | 7 |
| *Arctocephalus gazella* | Antarctic fur seal | 34.6 | 5520.0 | measurement | 16 | |
| | | 36.8 | 4817.7 | measurement | 3 | 7 |
| | | 39.4 | 3993.7 | measurement | 20 | 7 |
| | | 188.0 | 11898.6 | measurement | 8 | 7 |
| *Callorhinus ursinus* | Northern fur seal | 42.7 | 4117.6 | measurement | 18 | 7 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | 43.2 | 7297.7 | measurement | 18 | 7 |
| | | 51.1 | 8664.0 | measurement | 19 | |
| *Eumetopias jubatus* | Steller sea lion (female) | 247.0 | 20780.0 | estimate | 97 | |
| | Steller sea lion (male) | 656.0 | 39888.0 | estimate | 97 | |
| *Neophoca cinerea* | Australian sea lion | 83.5 | 9480.0 | measurement | 16 | |
| | | 84.5 | 13348.7 | measurement | 17 | |
| *Zalophus californianus* | CA sea lion | 78.0 | 9264.0 | measurement | 15 | |
| | | 81.7 | 9063.3 | measurement | 15 | 7 |
| | | | | | | |
| **Phocidae** | | | | | | |
| *Halichoerus grypus* | Grey seal | 168.0 | 4216.7 | captive | 80 | 7 |
| *Leptonychotes weddellii* | Weddell seal | 263.0 | 4669.0 | measurement | 49 | 7 |
| | | 350.0 | 10688.5 | measurement | 72 | 7 |
| | | 355.0 | 8863.0 | measurement | 51 | 7 |
| | | 355.0 | 8344.2 | measurement | 12 | |
| | | 355.0 | 12270.9 | measurement | 12 | |
| | | 425.0 | 12179.4 | measurement | 50 | 7 |
| *Mirounga angustirostris* | Northern elephant seal | 265.0 | 9700.0 | estimate | 81 | |
| | | 376.0 | 6641.7 | measurement | 57 | |
| *Mirounga leonina* | Southern elephant seal | 396.0 | 24123.9 | estimate | 44 | |
| *Pagophilus groenlandicus* | Harp seal | 95.0 | 2095.0 | captive | 42 | 7 |
| *Phoca vitulina* | Harbor seal | 63.0 | 4313.8 | captive | 24 | 7 |
| | | 87.5 | 4613.2 | measurement | 6 | 7 |
| | | 87.5 | 4613.2 | measurement | 6 | 7 |
| | | 93.0 | 12547.0 | measurement | 77 | 7 |
| | | 107.5 | 7361.8 | measurement | 14 | 7 |

## Terrestrial Mammals

| Scientific Name | Common Name | Mass (kg) | FMR (kcal d$^{-1}$) | Determination Type | Source (1) | Source (2) |
|---|---|---|---|---|---|---|
| **Carnivores** | | | | | | |
| **Canidae** | | | | | | |
| *Canis latrans* | Coyote | 10.4 | 1082.8 | measurement | 56 | 11 |
| *Canis lupus* | Timber wolf | 37.3 | 4248.0 | measurement | 64 | 65 |
| *Canis lycaon* | Eastern wolf | 37.3 | 4247.9 | measurement | 36 | 11 |
| *Lycaon pictus* | African wild dog | 25.0 | 3670.0 | measurement | 36 | 65 |
| *Vulpes cana* | Blanford's fox | 1.0 | 160.8 | measurement | 32 | 46 |
| *Vulpes macrotis* | Kit fox | 1.5 | 283.2 | measurement | 65 | 11 |
| *Vulpes rueppellii* | Rüppell's fox | 1.8 | 243.5 | measurement | 94 | 46 |
| *Vulpes velox* | Swift fox | 2.1 | 427.2 | measurement | 21 | 11 |
| *Vulpes vulpes* | Red fox | 4.3 | 574.1 | measurement | 98 | 46 |
| **Felidae** | | | | | | |
| *Lynx pardinus* | Iberian lynx | 12.7 | 795.0 | measurement | 2 | 11 |
| *Panthera leo* | Lion | 136.0 | 8813.7 | measurement | 83 | 11 |
| **Hyaenidae** | | | | | | |
| *Proteles cristatus* | Arardwolf | 8.5 | 440.5 | measurement | 93 | 65 |
| **Mustelidae** | | | | | | |
| *Lontra canadensis* | North American river otter | 7.8 | 1137.1 | measurement | 29 | 46 |
| *Martes americana* | American marten | 0.69 | 125.3 | measurement | 35 | 46 |
| *Martes pennanti* | Fisher | 4.4 | 277.3 | measurement | 74 | 11 |
| *Mustela nivalis* | Least Weasel | 0.11 | 51.7 | measurement | 58 | 11 |
| **Procyonidae** | | | | | | |
| *Bassariscus sumichrasti* | Ring-tailed cat | 0.75 | 113.3 | measurement | 13 | 11 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Ursidae** | | | | | | |
| *Ursus maritimus* | Polar bear | 306.4 | 10172.1 | measurement | 91 | 1 |
| **Non-Carnivores** | | | | | | |
| **Afrosoricida** | | | | | | |
| *Eremitalpa granti* | Grant's golden mole | 0.021 | 3.0 | | 85 | 46 |
| *Microgale dobsoni* | Shrew-tenrec | 0.043 | 18.5 | measurement | 90 | 65 |
| *Microgale talazaci* | Shrew-tenrec | 0.043 | 16.0 | measurement | 90 | 65 |
| **Artiodactyla** | | | | | | |
| *Antidorcas marsupialis* | Springbok | 43.3 | 5784.0 | measurement | 66 | 65 |
| *Cervus elaphus* | Red deer | 107.5 | 6053.8 | measurement | 40 | 46 |
| *Lama glama* | Llama | 48.0 | 3372.6 | measurement | 79 | 46 |
| *Odocoileus hemionus* | Mule deer | 40.0 | 5582.0 | measurement | 63 | 65 |
| *Odocoileus hemionus* | Mule deer | 67.1 | 9552.0 | measurement | 63 | |
| *Oryx leucoryx* | Arabian oryx | 84.1 | 3936.7 | measurement | 95 | 46 |
| *Rangifer tarandus* | Reindeer | 61.0 | 3834.4 | measurement | 37 | 46 |
| **Chiroptera** | | | | | | |
| *Anoura caudifer* | Tailed tailless bat | 0.011 | 12.6 | measurement | 43 | 46 |
| *Carollia brevicauda* | Silky short-tailed bat | 0.009 | 11.0 | measurement | 92 | 46 |
| *Carollia perspicillata* | Seba's short-tailed bat | 0.020 | 18.8 | measurement | 31 | 46 |
| *Eptesicus fuscus* | Big brown bat | 0.021 | 10.5 | measurement | 55 | 65 |
| *Glossophaga commissarisi* | Commissaris's long-tongued bat | 0.018 | 12.0 | measurement | 92 | 46 |
| *Macrotus californicus* | California leaf-nosed bat | 0.013 | 5.3 | measurement | 4 | 46 |
| *Myotis lucifugus* | Little brown bat | 0.009 | 7.2 | measurement | 54 | 65 |
| *Phyllostomus hastatus* | Greater spear-nosed bat | 0.076 | 32.1 | measurement | 53 | 46 |
| *Pipistrellus pipistrellus* | Pipistrelle | 0.007 | 7.0 | measurement | 75 | 65 |
| *Plecotus auritus* | Brown long-eared bat | 0.009 | 6.6 | measurement | 89 | 65 |
| *Syconycteris australis* | Common blossom bat | 0.017 | 18.4 | measurement | 33 | 46 |

| | | | | | | |
|---|---|---|---|---|---|---|
| **Lagomorpha** | | | | | | |
| *Lepus americanus* | Snowshoe hare | 1.4 | 236.7 | measurement | 86 | 46 |
| *Lepus californicus* | Black-tailed jackrabbit | 1.8 | 312.0 | measurement | 87 | 65 |
| | | | | | | |
| **Pilosa** | | | | | | |
| *Bradypus variegatus* | Brown-throated sloth | 4.2 | 151.8 | measurement | 68 | 46 |
| | | | | | | |
| **Primates** | | | | | | |
| *Alouatta palliata* | Mantled howler monkey | 6.3 | 550.2 | measurement | 67 | |
| *Aloutta palliata* | Mantled howler monkey | 8.4 | 683.2 | measurement | 67 | 65 |
| *Eulemur fulvus* | Common brown lemur | 1.8 | 142.8 | measurement | 88 | 46 |
| *Lemur catta* | Ring-tailed lemur | 2.3 | 148.8 | measurement | 88 | 46 |
| *Lepilemur ruficaudatus* | Red-tailed sportive lemur | 0.72 | 113.4 | measurement | 30 | 46 |
| *Microcebus murinus* | Gray mouse lemur | 0.061 | 22.7 | measurement | 84 | 46 |
| *Pongo pygmaeus* | Bornean orangutan | 62.6 | 1631.5 | measurement | 73 | 46 |
| | | | | | | |
| **Rodentia** | | | | | | |
| *Acomys cahirinus* | Common spiny mouse | 0.038 | 12.4 | measurement | 26 | 65 |
| *Acomys russatus* | Golden spiny mouse | 0.045 | 11.5 | measurement | 26 | 65 |
| *Ammospermophilus leucurus* | Antelope ground squirrel | 0.087 | 21.1 | measurement | 47 | 65 |
| *Aplodontia rufa* | Mountain beaver | 0.73 | 357.1 | measurement | 22 | 46 |
| *Arvicola amphibius* | European water vole | 0.083 | 33.4 | measurement | 39 | 46 |
| *Arvicola terrestris* | Water vole | 0.086 | 28.6 | measurement | 39 | 65 |
| *Cavia magna* | Greater guinea pig | 0.50 | 102.1 | measurement | 52 | 46 |
| *Clethrionomys glareolus* | Bank vole | 0.023 | 21.1 | measurement | 23 | 65 |
| *Clethrionomys rutilus* | Northern red-backed vole | 0.016 | 13.8 | measurement | 45 | 65 |
| *Dipodomys merriami* | Merriam's kangaroo rat | 0.034 | 11.4 | measurement | 59 | 65 |
| *Dipodomys microps* | Chisel-tooth kangaroo rat | 0.057 | 20.3 | measurement | 59 | 65 |
| *Gerbillus allenbyi* | Allenby's gerbil | 0.023 | 8.5 | measurement | 28 | 65 |
| *Gerbillus henleyi* | Northern pygmy gerbil | 0.009 | 6.4 | measurement | 27 | 65 |
| *Gerbillus pyramidum* | Greater Egyptian gerbil | 0.032 | 10.8 | measurement | 28 | 65 |

| | | | | | | |
|---|---|---|---|---|---|---|
| *Lemmus sibiricus* | Siberian brown lemming | 0.055 | 48.2 | measurement | 71 | 46 |
| *Marmota flaviventris* | Yellow-bellied marmot | 3.2 | 583.2 | measurement | 82 | 65 |
| *Meriones crassus* | Jird | 0.069 | 15.6 | measurement | 27 | 65 |
| *Microtus agrestis* | Field vole | 0.027 | 18.7 | measurement | 23 | 65 |
| *Microtus arvalis* | Meadow mouse | 0.020 | 21.6 | measurement | 23 | 65 |
| *Microtus pennsylvanicus* | Meadow vole | 0.036 | 24.1 | measurement | 5 | 46 |
| *Mus domesticus* | Wild house mouse | 0.015 | 11.3 | measurement | 62 | 65 |
| *Perognathus formosus* | Long-tailed pocket mouse | 0.018 | 10.8 | measurement | 61 | 65 |
| *Peromyscus crinitus* | Cactus mouse | 0.013 | 9.4 | measurement | 60 | 65 |
| *Peromyscus leucopus* | White-footed mouse | 0.019 | 8.5 | measurement | 76 | 46 |
| *Peromyscus maniculatus* | Deer mouse | 0.018 | 12.8 | measurement | 41 | 65 |
| *Praomys natalensis* | Multi-mammate mouse | 0.057 | 20.8 | measurement | 38 | 65 |
| *Psammomys obesus* | Fat sand rat | 0.17 | 39.6 | measurement | 25 | 65 |
| *Sciurus carolinensis* | Eastern gray squirrel | 0.59 | 139.3 | measurement | 10 | 46 |
| *Sekeetamys calurus* | Bushy-tailed jird | 0.041 | 10.6 | measurement | 26 | 65 |
| *Spermophilus parryi* | Arctic ground squirrel | 0.63 | 196.1 | measurement | 23 | 65 |
| *Spermophilus saturatus* | Golden-mantled ground squirrel | 0.21 | 54.2 | measurement | 48 | 65 |
| *Tamias striatus* | Eastern chipmunk | 0.096 | 34.4 | measurement | 76 | 46 |
| *Thomomys bottae* | Botta's pocket gopher | 0.10 | 31.2 | measurement | 34 | 65 |
| | | | | | | |
| **Soricomorpha** | | | | | | |
| *Sorex araneus* | Common shrew | 0.008 | 13.0 | measurement | 70 | 46 |

### A.2.2 Data sources

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