

Copyright by The University of Chicago Press

Juvenile Southern Elephant Seals Exhibit Seasonal Differences in Energetic Requirements and Use of Lipids and Protein Stores

Iain C. Field, Corey J. A. Bradshaw, Harry R. Burton, and Mark A. Hindell

Physiological and Biochemical Zoology, Vol. 78, No. 4 (July/August 2005), pp. 491-504

Published by: [The University of Chicago Press](#)

Article DOI: 10.1086/430227

Article Stable URL: <http://www.jstor.org/stable/10.1086/430227>



Juvenile Southern Elephant Seals Exhibit Seasonal Differences in Energetic Requirements and Use of Lipids and Protein Stores

Author(s): Iain C. Field, Corey J. A. Bradshaw, Harry R. Burton, and Mark A. Hindell

Source: *Physiological and Biochemical Zoology*, Vol. 78, No. 4 (July/August 2005), pp. 491-504

Published by: [The University of Chicago Press](#)

Stable URL: <http://www.jstor.org/stable/10.1086/430227>

Accessed: 11/09/2013 22:17

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press is collaborating with JSTOR to digitize, preserve and extend access to *Physiological and Biochemical Zoology*.

<http://www.jstor.org>

Juvenile Southern Elephant Seals Exhibit Seasonal Differences in Energetic Requirements and Use of Lipids and Protein Stores

Iain C. Field^{1,2,*}

Corey J. A. Bradshaw^{1,3}

Harry R. Burton²

Mark A. Hindell³

¹Antarctic Wildlife Research Unit, School of Zoology, University of Tasmania, Private Bag 05, Hobart, Tasmania 7001, Australia; ²Australian Antarctic Division, Channel Highway, Kingston, Tasmania 7050, Australia; ³Key Centre for Tropical Wildlife Management, Research School of Environmental Studies, Charles Darwin University, Darwin, Northern Territory 0909, Australia

Accepted 11/30/2004; Electronically Published 5/26/2005

ABSTRACT

Growing juvenile animals undergo many morphological, physiological, and behavioural changes that influence their energetic requirements, patterns of energy use, and ultimately, their survival and reproductive success. We examined changes in mass loss and body composition of juvenile southern elephant seals (1- and 2-yr-olds) during their two annual haul-outs. At the start and end of the midyear and molt haul-outs, we caught, weighed, and measured 41 and 14 seals, respectively. We measured blubber depth using ultrasound to estimate body composition (lean and adipose tissue mass). Using energy densities of the adipose and lean tissue, we calculated total, lean, and adipose mass changes and energy expenditure. While molting, juvenile seals used more energy than during the midyear, which is related to the increased use of lean tissue for hair and skin regeneration. The amount of energy used increases with mass as individuals mature. We found sexual differences in energy use where females retained greater fat reserves than males by utilizing more lean tissue. These differences are most likely related to haul-out function and behavior, growth, and earlier development of females toward sexual maturity.

Introduction

Physiological flexibility allows long-lived individuals to adapt to changes in energetic requirements throughout their lifetime, and generally, juveniles demonstrate the greatest flexibility in metabolic rates and pathways (Post and Parkinson 2001). Nonetheless, there is a paucity of research on intraspecific differences in metabolic rates (Nagy 2000), and even fewer studies on marine mammals, a group where juvenile body size has been shown to influence future reproductive success (Le Boeuf and Reiter 1988; Stearns 1992) and thermoregulatory capacity. Furthermore, the evidence suggests that juveniles have the greatest energetic demands for growth as they develop toward maturity (Costa and Williams 1999; Boyd 2002). As such, in capital-breeding marine mammals, it has been hypothesized that there should be differences in energy management between the sexes during maturation.

Southern elephant seals (*Mirounga leonina*) are one of the most morphologically and physiologically extreme mammal species. They are highly adapted for a marine existence and spend more than 80% of their annual cycle far from land while foraging for deep-dwelling prey (>200 m). They also demonstrate some of the longest fasting periods of any pinniped while on land (Le Boeuf and Laws 1994). Southern elephant seals have a circumpolar distribution throughout the Southern Ocean, are wide ranging (capable of traveling in excess of 5,000 km from their breeding and molting areas; Hindell and McMahon 2000), dive to extreme depths (>1,500 m; Hindell 2002), and are important apex predators that consume large quantities of prey to maintain and provision themselves for successful breeding (Boyd et al. 1994; Knox 1994; Hindell et al. 2003).

The Macquarie Island population of southern elephant seals (~80,000 individuals), representing approximately 10% of the species' total abundance (Le Boeuf and Laws 1994, McMahon 2003), has been declining since the 1950s (Hindell 1991; McMahon et al. 2003, 2004). The most plausible ultimate cause of the decline is food limitation (Hindell 1991; McMahon et al. 2003, 2004). McMahon et al. (2003) demonstrated that changes in juvenile survival (1–4 yr) affected the rate of population change more than other demographic parameters (e.g., adult survival and fecundity). Therefore, it appears that juvenile survival to reproductive age is closely related to the ability of juveniles to find and assimilate food resources and to allocate these energy reserves to growth and eventual reproduction.

Most metabolic and physiological studies have focused on adults when ashore or at sea (Boyd et al. 1993, 1999; Slip et

* Corresponding author; e-mail: icfield@utas.edu.au.

al. 1994; Hindell et al. 2000) or on the interactions between mothers and pups (Arnbom et al. 1993; Hindell and Slip 1997; Biuw 2003), with little attention given to the ontogeny of metabolic changes after the first year of life (Hindell and Burton 1987). As seals grow, an increase in absolute metabolic rate is expected because of the increasing body size, but there is also likely to be an increased demand for somatic growth. There may also be reductions in overall metabolic requirements caused by increased efficiency in foraging behavior, energy assimilation, and energy use (Schmidt-Nielsen 1997). Also, a number of studies have shown that body composition (the amount of lipid and protein stores that are available for catabolism) is important in the use of energy reserves where seals with greater amount of lipids will preferentially catabolize lipids. Elephant seals, like most mammals, use lipid reserves for energy, sparing protein while fasting (Houser and Costa 2001; Noren et al. 2003), but also need to retain lipids (fat sparing) as a component of blubber required for thermoregulation (Worthy and Lavigne 1987), buoyancy, and hydrodynamic streamlining (Webb et al. 1998).

As seals grow, there may be significant differences between the sexes (Bell et al. 1997) in both the amount of energy used and the tissue source from which it is derived, given that females demonstrate earlier sexual development relative to male peers (McMahon et al. 1997; Boness et al. 2002; McMahon 2003). Precocious development appears to aid primiparous females (Siervogel et al. 2003) because of earlier lactation requirements (~3–4 yr old; McMahon et al. 2003), while males continue greater somatic growth until reaching maturity later (~8–10 yr old; McCann 1980) to increase reproductive potential by maximizing body size necessary for extreme male-male competition. Therefore, precocious development should result in females having a tendency to spare lipid and burn more protein when compared with males of the same age.

The timing of terrestrial haul-outs also changes with age (Carrick et al. 1962; Hindell and Burton 1988; Kirkman et al. 2001; Wheatley 2001; Field et al. 2005). After juveniles go to sea following their annual molt (~32 d from approximately December to January), they return to land during the winter (~24 d from approximately April to August). The function of this winter, or “midyear,” haul-out is unclear, but it may be because of physiological restrictions, development, parasite reduction, social interactions, reduction of intraspecific competition, or simply to rest (Carrick et al. 1962; Condy 1979; Ling and Bryden 1981; Burton 1985; Neumann 1999; Field et al. 2005). The molting and midyear haul-outs clearly serve different functions, and it is probable that juvenile seals expend more energy during the molt because of the elevated energetic demands associated with the production of new epidermis and hair and increased rates of heat loss. Regardless of the function of the midyear haul-out, if we assume that it is the same for all juveniles, then differences in metabolic rate between the sexes may be caused by developmental differences. These dif-

ferences may also be apparent between haul-out periods when females might reduce metabolic rates to conserve energy reserves for growth, maintenance, and provisioning for breeding and fasting.

In this article, we test the hypothesis that during the juvenile years (1–3 yr), metabolic rate changes in response to differences in the way energy is stored and used as a function of growth and development and that these patterns are also influenced by the function of the specific terrestrial haul-outs (i.e., midyear or molt). Specifically, we examine changes in (1) rates of mass loss, (2) body composition, and (3) energy use among different age groups, sexes, and haul-out periods (molt and midyear). Observed trends are discussed in terms of the proportions of lipid and protein used to derive the energy needed during a fast. We predict that from precocious development, females will have reduced metabolic rates to those of males of similar age that allow females to conserve energy and increase fecundity.

Methods

Between November 1999 and February 2001, 55 juvenile southern elephant seals were captured as part of a long-term demographic study of the population on Macquarie Island (Hindell et al. 1994b; McMahon et al. 2003). Data for this study were collected with Australian Antarctic Animal Ethics Committee approval (Antarctic Scientific Advisory Committee 2265 and 1171) and with Tasmanian Parks and Wildlife Service permits. Seals were caught and immobilized as they returned for their molt and midyear haul-outs and then again at the end of the haul-outs before returning to sea. Seals ranged in age from 13 to 33 mo at the time of capture and were subsequently allocated into 1- and 2-yr-old age groups.

Seals were caught by hand by placing a canvas bag over the seal's head (McMahon et al. 2000) and administering anesthesia intravenously, using prescribed doses (Field et al. 2002) of a combined 1 : 1 mixture of tiletamine and zolazepam (Telazol, Forte Dodge, Castle Hill). Once anaesthetized, the seals were weighed using a digital scale (± 1 kg; Dillon ED-2000, Salter Weigh-Tronix, Victoria) and measured (± 1 cm). Serial length and girth measurements were made to calculate total body volume (Gales and Burton 1987). Morphometric measurements were made across seven sections (Fig. 1), with the head and hips to the base of the tail forming cones and the rest of the body sections forming truncated cones (Field et al. 2002). Measures of blubber thickness corresponding with the girth measurements along the seal's dorsal side were obtained using an ultrasound backfat depth system (A-Scan Plus, Sis-Pro, Woodbury, MN). From these morphometric and ultrasonic measurements, total blubber and lean tissue volumes were calculated. It should be noted that this method, though valid (Gales and Burton 1987; Slip et al. 1992a; Worthy et al. 1992; Webb et al. 1998; Mellish et al. 2004), has been shown in some other species to have discrepancies with other techniques, and

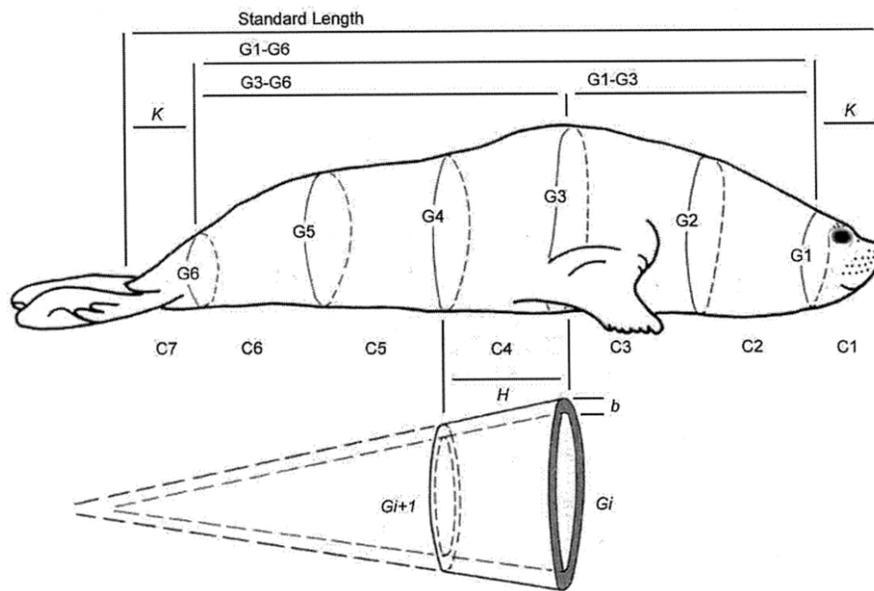


Figure 1. Morphometric measurements used in the calculation of blubber volume. G1–G6 represents the circumference of the body at sites 1–6, thus creating seven cones (five truncated and two terminal cones). The depth of blubber (b) was assessed at the dorsal surface of all six sites and used to calculate total blubber volume (after Field et al. 2002).

absolute values of protein use may be overestimated (Worthy and Lavigne 1983); however, in a relative study such as ours with equal variability across sample groups, this method is valid for within-sample comparisons.

This method assumed that individuals were circular in cross section, such that the diameter for any cross section was equivalent to the circumference divided by π . We also assumed that all the blubber lies in the hypodermis and over the whole body and that the flippers contain insignificant amounts of subcutaneous fat (Field et al. 2002). Total blubber mass (Slip et al. 1992b; Webb et al. 1998) was calculated by multiplying the blubber volume by the density of blubber, taken as 0.95 g cm^{-3} (Gales and Burton 1987). Some past studies (Slip et al. 1992b; Webb et al. 1998) measured 18 blubber depths, whereas we have measured only six. To address the variability between using six versus 18 blubber depth measurements for calculating adipose tissue volume, we used data from 311 other seals for which we had taken 18 ultrasound measurements (these seals were not sampled longitudinally and were therefore not included in this study). We used linear regression to model variability between lean volumes calculated using six (vol 6) and 18 (vol 18) ultrasound measurements. We found a strong positive relationship ($\text{vol } 18 = 1.0144 \times \text{vol } 6 + 0.0036$; $r^2 = 0.999$). Although the slope of this relationship was close to 1.0, we used this (1.0144) as a correction factor in calculating adipose tissue volume (Fig. 2). This technique has shown strong agreement with isotopic techniques in the calculation of body composition (Webb et al. 1998), with a mean error of $0.01\% \pm 4.25\%$ and with in situ measurements of blubber

depth (Mellish et al. 2004). Lean body mass was calculated by subtracting the blubber mass from the total body mass.

Indices of Body Composition

The following assumptions were made to convert measurements into the amounts of fat and protein present: (1) all lipids metabolized by the seals were accounted for by the changes in total blubber mass, which contains 95% of the dissectible fat (Bryden 1967), and any metabolized protein was derived from changes in total lean mass; (2) energy densities of pure fat and protein are 39.5 MJ kg^{-1} and 17.99 MJ kg^{-1} , respectively (Reilly and Fedak 1990; Schmidt-Nielsen 1997); (3) lean tissue consists of 27% protein and 73% water (Pace and Rathbun 1945; Slip et al. 1992b); and (4) the animal's state of hydration remains constant over the fasting period (Ortiz et al. 1978). Thus,

$$\text{energy expenditure} = \text{BML} \times E_{\text{lipid}} + \text{LML} \times k_{\text{lean}} \times E_{\text{lean}},$$

where BML = blubber mass loss, LML = lean mass loss, E_{lipid} = energy provided from lipid mass loss (39.5 MJ kg^{-1}), k_{lean} = proportion of lean mass that is protein (0.27), and E_{lean} = energy provided from protein mass loss (17.99 MJ kg^{-1}).

Body size is fundamental in determining metabolic rate by standard allometry (Kleiber 1975; Schmidt-Nielsen 1997) where there is an interspecific increase in body mass with age ($r^2 = 0.773$; Fig. 3). Therefore, to remove variability because of the size of the individual, we used mass as a covariate in

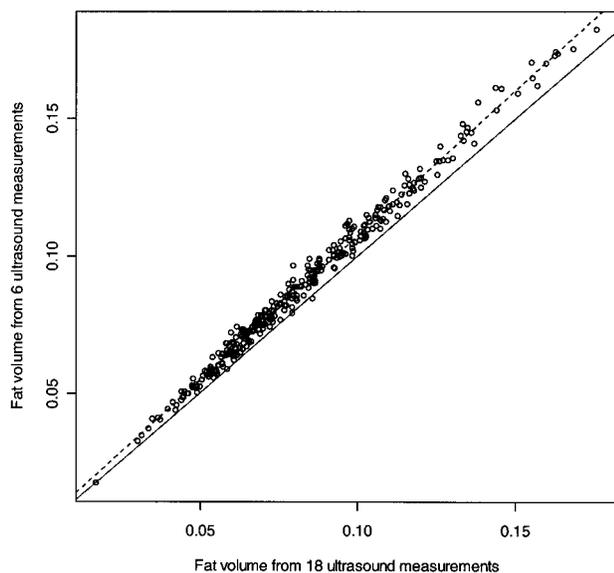


Figure 2. Relationship between volume of fat calculated using 18 and six ultrasound measurements, showing the best-fit linear regression line (dotted line; $r^2 = 0.988$) and the reference line (solid line; $y = x$).

our analyses. To describe the overall changes in body composition, we chose to compare overall mass loss, lean-tissue loss, and adipose-tissue loss. Before any comparison of energy use could be made, we determined whether the seals had similar proportions of adipose to lean tissue at the start and end of a haul-out to find out whether all juveniles had similar energy reserves available to them. Differences in body composition between the start and end of a haul-out were used to measure the daily total energy expended. To examine whether seals differed in the relative amount of energy derived from various body components, we also calculated the proportion of total energy derived from lipids in their fat stores.

In addition to the availability of specific substrates, there are limited amounts of body lipid and protein that can be used for energy production without causing acute loss of tissue (i.e., the breakdown of organ tissue or reduction in heat insulation; Cahill et al. 1979; Cherel et al. 1987; Reilly 1989). Therefore, we calculated the lean mass loss as a proportion of lean mass at the start of a haul-out to investigate to what degree individuals engage in protein metabolism during the course of the haul-out fast. We also calculated adipose tissue mass as a proportion of body mass at the end of a haul-out to examine whether individuals retain enough fat for energy reserves and thermoregulation (Cahill et al. 1979; Fedak et al. 1996; McConnell et al. 2002; Biuw 2003).

Statistical Analysis

We compared 1- and 2-yr-old seals, sexes, and the two haul-outs using general factorial generalized linear models (GLM)

in the R package (ver. 1.8.1; Ihaka and Gentleman 1996), including body mass as a covariate for the different response variables. These models also tested for the effect of main factors (e.g., age, sex, and haul-out) and all two-way and three-way interactions with mass on the response variables. Examination of the residuals for all models indicated that a Gaussian family error distribution with a log-link was the most appropriate model structure for the input data.

There was no a priori reason to assume a single model to describe the contribution of terms and their interactions to the response variables, so we used a form of model selection with sample-size-corrected Akaike Information Criteria (AICc) to select the most parsimonious models (Lebreton et al. 1992; Burnham and Anderson 1998). AICc is calculated as

$$\text{AICc} = \text{LL} + 2K + \frac{2K(K+1)}{(n-K-1)},$$

where $\text{LL} = -2 \log$ likelihood calculated from the mean squared error and the Type III sum of squares error for each general factorial GLM, K = number of model parameters, and n = sample size. AICc values are then ranked on a relative scale from 0 (poor) to 1 (good; i.e., model weight; Burnham and Anderson 1998). Thus, best-fit models have the lowest AICc value and the highest model weight (Lebreton et al. 1992). To test between the most parsimonious models, only the top models when summed that contributed to greater than 0.5 of the total AICc model weights were considered. To determine the

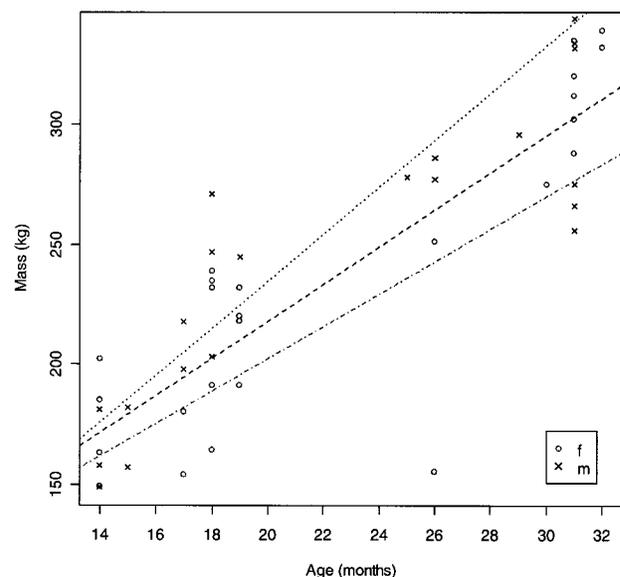


Figure 3. Change in mass for 1- and 2-yr-old juvenile elephant seals, with age in months, showing the best-fit linear regression lines (the dashed line for model includes age, sex, and an age \times sex interaction [$r^2 = 0.773$], the dotted line is for males [$r^2 = 0.66$], and the dotted-and-dashed line is for females [$r^2 = 0.636$]).

effect of any term seen to be significant in selected models, we used a χ^2 analysis of deviance. The results of this model selection are shown as the ranked, most parsimonious models, their individual AICc weight, the significance terms of each model, and specific-term tests using analysis of deviance. Finally, from these models, we used a predictive model averaging procedure to determine the magnitude of the effect of the significant terms, keeping all other dependent variables constant (Burnham and Anderson 1998). Here, the coefficients for significant terms in the top competing models were modified by their AICc weights and averaged over all models considered to provide model-averaged response predictions.

Results

The overall average mass loss per day for the molt and midyear haul-outs were 2.1 ± 0.5 and 2.2 ± 0.6 kg d⁻¹ over 32.2 ± 5.6 and 24 ± 3.6 d, respectively. Molting individuals were younger and smaller than those in the midyear because they were caught earlier in the year. There were differences between haul-outs, ages, and sex in all mass loss parameters (Table 1) and in the amounts and metabolic sources of energy (Table 2) used by the different age groups and sexes that are described below.

Overall Mass Loss Rate

There were significant differences in the overall mass loss rate in the different haul-outs and a positive relationship with body mass. The candidate models from our model selection showed strong mass and haul-out effects, which were both significant in our analysis of deviance (mass, $\chi_1^2 = 71.665$, $P < 0.001$; haul-out, $\chi_1^2 = 0.694$, $P = 0.021$; Table 3). From our predictive model averaging procedure using all contributing models and keeping mass, sex, and age constant, the overall mass loss rate was 12.6% greater on average in the molt than in the midyear haul-out.

Lean Tissue Loss Rate

For the rate of lean tissue loss, there were significant differences between sexes and haul-outs and a positive relationship with mass. The candidate models showed strong mass, sex, and haul-out effects, which were all significant in our analysis of deviance (mass, $\chi_1^2 = 17.222$, $P < 0.001$; sex, $\chi_1^2 = 5.064$, $P = 0.029$; haul-out, $\chi_1^2 = 5.140$, $P = 0.028$; Table 3). From our predictive model averaging procedure using all contributing models and keeping all dependent variables constant except haul-out, loss rate in the molt lean tissue was 31.2% higher on average than in the midyear haul-out. Also, there was a significant difference between the sexes; thus, keeping all dependent variables in the model averaging constant except for sex, females used on average 15.1% more lean tissue than males of similar size and age during the same haul-out.

Adipose Tissue Loss Rate

For the rate of adipose tissue loss, there were significant differences between the sexes and a positive relationship with mass. The candidate models showed strong mass and sex effects, which were both significant in our analysis of deviance (mass, $\chi_1^2 = 27.605$, $P < 0.001$; sex, $\chi_1^2 = 15.234$, $P < 0.001$; Table 3). Keeping all dependent variables constant except sex, females used on average 15.7% less adipose tissue than males of similar size and age during the same haul-out.

Ratio of Adipose : Lean Tissue

At the start of the haul-outs, the ratio of adipose : lean tissue was significantly different between haul-outs and negatively related to mass. The candidate models showed strong mass and haul-out effects, which were both significant in the analysis of deviance (mass, $\chi_1^2 = 15.447$, $P < 0.001$; haul-out, $\chi_1^2 = 43.508$, $P < 0.001$; Table 3). On their return, seals had 18.9% higher proportions of adipose : lean tissue on average at the start of the midyear (Fig. 4) than at the start of the molt (keeping mass, age, and sex constant). When keeping all dependent variables constant except for mass, an increase in mass decreased the proportion of adipose : lean tissue.

For the ratio of adipose : lean tissue at the end of a haul-out, there were significant differences between sexes and between haul-outs (Fig. 4). The candidate models showed strong haul-out, sex, and sex \times mass interaction effects (analysis of deviance: haul-out, $\chi_1^2 = 62.258$, $P < 0.001$; sex, $\chi_1^2 = 13.888$, $P < 0.001$; sex \times mass, $\chi_1^2 = 5.931$, $P = 0.018$; Table 3). The sex \times mass interaction demonstrated a greater increase in the proportion adipose : lean tissue for females with an increase in mass than for males. Keeping all dependent variables constant except for sex, females had on average 13.6% higher proportions of adipose : lean tissue than males of similar size and age during the same haul-out. In the midyear the seals had 30.7% higher proportions of adipose : lean tissue.

Daily Energy Expenditure

The rate of daily energy expenditure showed significant sex and mass differences (analysis of deviance: mass, $\chi_1^2 = 40.474$, $P < 0.001$; sex, $\chi_1^2 = 13.647$, $P < 0.001$; Table 3). On average, males had a 13.4% greater daily energy expenditure rate than females, and there was a positive increase in daily energy expenditure with an increase in mass (Fig. 5).

Proportion of Total Energy Derived from Lipids

The proportion of energy derived from lipid metabolism was significantly different between sexes and haul-outs. The candidate models showed mass, age, haul-out, and sex effects, but only sex and haul-out were significant according to the analysis

Table 1: Age and sex differences in mass loss for juvenile southern elephant seals in their two annual haul-outs, including proportion of fat and lean mass at the start and end of the molt and midyear haul-outs

Haul-Out, Age, and Sex	Days	Mass (kg)	End Mass (kg)	Mass Loss Rate (kg ⁻¹ d ⁻¹)	Lean Mass (kg)	End Lean Mass (kg)	Lean Mass Loss Rate (kg ⁻¹ d ⁻¹)	Fat Mass (kg)	End Fat Mass (kg)	Fat Mass Loss Rate (kg ⁻¹ d ⁻¹)	Ratio of Fat : Lean	End Ratio of Fat : Lean
Molt:												
1:												
F (4)	31.75	174.75	119.50	1.75	126.76	99.26	.87	47.99	20.24	.88	.38	.20
F (4)	2.63	23.44	17.06	.22	18.05	14.07	.15	5.59	3.00	.07	.02	.00
M (5)	25.40	165.40	123.60	1.66	119.30	103.78	.61	46.10	19.82	1.05	.39	.19
M (5)	4.28	15.11	4.22	.44	9.29	3.71	.28	6.46	2.98	.19	.03	.03
2:												
F (2)	32.00	203.00	133.50	2.15	149.74	109.74	1.23	53.26	23.76	.92	.36	.22
F (2)	8.49	67.88	44.55	.16	50.92	36.59	.12	16.96	7.96	.04	.01	.00
M (3)	33.33	280.33	200.33	2.40	204.42	167.55	1.11	75.91	32.78	1.29	.37	.20
M (3)	.58	4.93	7.77	.27	4.11	2.71	.16	7.89	5.80	.18	.04	.03
All:												
(14)	29.86	198.07	140.29	1.91	144.02	117.01	.88	54.05	23.28	1.03	.38	.20
(14)	5.01	51.95	36.25	.42	38.44	30.26	.31	14.06	6.57	.21	.03	.02
Midyear:												
1:												
F (12)	22.75	207.33	169.17	1.68	141.53	128.34	.58	65.80	40.82	1.10	.47	.32
F (12)	2.18	29.96	26.31	.26	21.09	18.89	.29	9.89	9.16	.25	.04	.05
M (6)	23.50	230.33	186.33	1.88	157.77	143.99	.59	72.57	42.34	1.30	.46	.30
M (6)	2.74	28.61	34.29	.39	22.82	28.40	.50	6.58	7.60	.25	.04	.04
2:												
F (8)	22.88	312.88	263.88	2.15	218.06	194.38	1.03	94.81	69.49	1.11	.43	.36
F (8)	1.73	23.18	23.22	.36	15.77	17.29	.33	9.21	8.58	.13	.03	.04
M (15)	26.27	342.80	280.67	2.36	241.64	219.34	.86	101.16	61.33	1.50	.42	.28
M (15)	5.04	57.32	48.42	.40	43.69	39.34	.28	15.50	10.69	.26	.04	.03
All:												
(41)	24.17	280.85	230.95	2.05	195.47	176.81	.77	85.39	54.14	1.28	.44	.31
(41)	3.78	72.40	61.96	.45	53.73	48.98	.37	19.54	14.96	.29	.04	.05

Note. Data reported as means with SD.

Table 2: Age and sex differences in the energy derived from fat and lean mass metabolism during the molt and midyear haul-outs and the proportion of lean mass to start lean mass and fat mass as a proportion of end body mass for juvenile southern elephant seals

Haul-Out, Age, and Sex	Energy from Fat (39.5 MJ kg ⁻¹)	Energy from Protein (17.99 MJ kg ⁻¹)	Daily Energy Expenditure (MJ d ⁻¹)	Percentage of Energy from Fat	Percentage of Energy from Protein	End Fat Mass as a Proportion of End Mass	Proportion of Lean Mass Loss to Start Lean Mass
Molt:							
1:							
F (4)	34.58	4.23	38.81	89.15	10.85	.17	.22
F (4)	2.81	.72	3.49	1.03	1.03	.00	.01
M (5)	41.59	2.97	44.55	93.58	6.42	.16	.13
M (5)	7.61	1.37	8.62	2.57	2.57	.02	.06
2:							
F (2)	36.22	5.99	42.21	85.82	14.18	.18	.27
F (2)	1.51	.59	2.09	.69	.69	.00	.01
M (3)	51.03	5.37	56.40	90.41	9.59	.16	.18
M (3)	7.12	.80	7.33	1.50	1.50	.02	.02
All:							
(14)	40.84	4.28	45.12	90.53	9.47	.17	.18
(14)	8.19	1.49	8.79	3.20	3.20	.02	.06
Midyear:							
1:							
F (12)	43.46	2.81	46.27	93.57	6.43	.24	.09
F (12)	9.81	1.41	9.15	3.46	3.46	.03	.04
M (6)	51.19	2.84	54.03	94.40	5.60	.23	.09
M (6)	9.73	2.43	8.39	4.60	4.60	.02	.08
2:							
F (8)	43.90	5.02	48.93	89.68	10.32	.26	.11
F (8)	5.30	1.62	5.55	3.19	3.19	.02	.04
M (15)	59.26	4.19	63.45	93.30	6.70	.22	.09
M (15)	10.31	1.36	10.55	2.17	2.17	.02	.02
All:							
(41)	50.46	3.75	54.21	92.84	7.16	.24	.10
(41)	11.53	1.78	11.52	3.46	3.46	.03	.04

Note. Data reported as means with SD.

Table 3: Candidate models (generalized linear models) describing the contribution of terms and their interactions (sample-size-adjusted Akaike Information Criterion weight; AICcwt), where significance of terms are shown in bold, to the response variables and significance of terms (analysis of deviance between models) for juvenile southern elephant seals incorporating body mass (m), sex (s), age (a), and haul-out (h)

Response Variable (Sum of All Model Weights) and Model Terms	AICcwt	Significant Terms from Analysis of Deviance
Mass loss rate (.68686):		Mass***, haul-out*
m + h	.21879	
m + h + m × h	.11334	
m + a + h	.07332	
m + h + s	.07289	
m + a + h + a × h	.05323	
Lean mass loss rate (.55613):		Mass***, haul-out**, sex*
M + h + s	.09049	
m + a + h + s	.08357	
a + h + s	.04276	
a + h	.03929	
m + h + s + m × h	.03799	
m + a + h + s + a × s	.03209	
m + h + s + s × h	.03175	
m + h + s + m × s	.03169	
m + a + h + s + m × h	.02931	
m + a + h + s + a × h	.02912	
m + a + h + s + m × a	.02828	
m + a + h	.02735	
Fat mass loss rate (.54568):		Mass***, sex***
m + a + s	.09079	
m + a + s + m × s	.08967	
m + a + s + a × s	.06305	
m + h + s + m × s	.05801	
m + a + h + s + m × s	.04707	
m + s + m × s	.04461	
m + a + h + s	.04399	
m + a + s + m × a + m × s	.03947	
Start ratio of fat : lean mass (.69067):		Mass***, haul-out***
m + h	.20647	
m + h + m × h	.12929	
m + a + h	.07776	
m + h + s	.06574	
m + a + h + m × h	.05236	
End ratio of fat : lean mass (.84935):		Haul-out***, sex***, mass × sex*
m + h + s + m × s	.32388	
m + a + h + s + m × s	.11432	
m + h + s + m × h + m × s	.10623	
Daily energy expenditure rate (.73807):		Mass***, sex***
m + s + m × s	.10443	
m + a + s + m × s	.09974	
m + a + s	.09039	
m + s	.06599	
m + a + s + a × s	.05756	
m + h + s + m × s	.05605	
m + a + s + m × a + m × s	.04366	
Percentage of energy from fat (.55699):		Mass*, haul-out**, sex***
a + h + s	.14001	
a + h + s + s × h	.08171	
a + h + s + a × s	.07205	
a + h + s + a × s + s × h	.05359	
m + a + h + s	.04835	
a + h + s + a × h	.04268	
m + h + s	.03422	
m + h + s + m × s + s × h	.02961	

* $P < 0.5$.
 ** $P < 0.01$.
 *** $P < 0.001$.

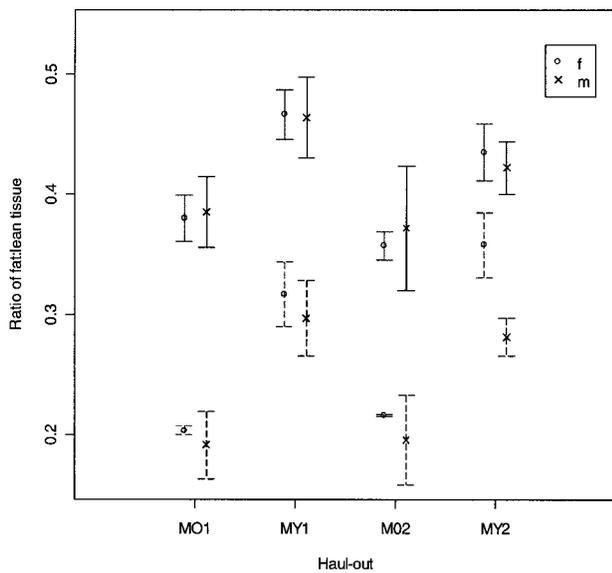


Figure 4. Proportion of fat to lean mass at the start (*solid lines*) and end (*dashed lines*) of their moult and midyear haul-outs ($\bar{X} \pm 2$ SE) for juvenile southern elephant seals, where MO1 and MO2 denote moult and MY1 and MY2 denote midyear haul-outs for 1- and 2-yr-old seals, respectively.

of deviance (haul-out, $\chi_1^2 = 8.865$, $P = 0.004$; sex, $\chi_1^2 = 14.124$, $P < 0.001$; Table 3). Seals decreased adipose reserves more (3.9%) during the midyear than during the moult (Table 2). There were also significant differences between the sexes, with males decreasing their adipose reserves more (3.7%) than females.

Lean Mass Loss as a Proportion of Start Lean Mass

The lean mass loss as a proportion of start lean mass was important to assess because it addresses whether seals were using more proteinaceous tissue than can be used without overfasting (defined as using $>30\%$ of original lean mass; Cahill et al. 1979; Cherel et al. 1987; Reilly 1989). From our results, juveniles used a greater proportion of their lean mass during the moult than during the midyear haul-out, and molting females used a greater proportion of their lean tissue than molting males, but they used similar proportions during the midyear haul-out (Table 2). However, none of the seals used $>30\%$ of their original lean tissue mass during either haul-out.

Proportion of End Adipose Mass to the End Body Mass

The proportion of end adipose mass to end body mass (percent body composition as fat) of the seal is, again, important in understanding whether juvenile seals are overfasting because this will influence the ability to thermoregulate when returning to sea. The seals used a greater proportion of their adipose in

the moult than in the midyear (Table 2), and males used greater proportions than females; however, even in the moult when most adipose tissue is used, no individuals had a body composition of less than 10% adipose tissue (Cahill et al. 1979; Cherel et al. 1987; Reilly 1989).

Discussion

Juvenile animals face an uncertain future as they approach maturity, undergoing many morphological, physiological, and behavioral changes that influence their energetic requirements and patterns of energy use (Post and Parkinson 2001). As juveniles grow, they experience increased absolute energetic demands required for the production of new tissues (Larner 1971; Robbins 1993; Schmidt-Nielsen 1997), and some species such as pinnipeds also need to store some energy for future use (Costa and Williams 1999; Boyd 2002). If these increasing demands are not met, this may result in a lower probability of survival or lower lifetime fecundity because of delayed age at first breeding (Brafeld and Llewellyn 1982). It is therefore likely that growing mammals will employ a range of energetic strategies in parallel to their changing requirements and environment (Wieser 1994) that could be identified through changes in body composition.

In summary, our data show that (1) in the moult, the seals use more energy than in the midyear, which is related to the increased use of lean tissue and to their body composition before the haul-out, and (2) there are sexual differences in energy use where females used less adipose but more lean tissue than males. Overall, juvenile mass loss rates during the moult

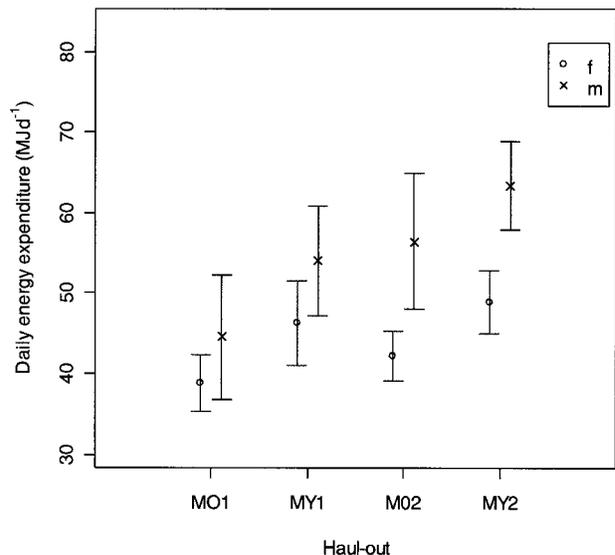


Figure 5. Daily energy expenditure ($\bar{X} \pm 2$ SE) for juvenile southern elephant seals, where MO1 and MO2 denote moult and MY1 and MY2 denote midyear haul-outs for 1- and 2-yr-old seals, respectively.

were in the range of those described in other studies of adult elephant seals during their molt (Worthy et al. 1992; Boyd et al. 1994; Hindell et al. 1994a). Although data are available for allometric comparison with adult southern elephant seals and other seal species, we limited our analyses to direct comparisons within the juvenile component of the population.

Seasonal Differences and Haul-Out Function

Seasonal differences in body condition (Post and Parkinson 2001) and metabolic rates are common in many species because of both intrinsic and extrinsic factors, but these differences may not affect all age groups identically. Intrinsic differences may be attributed to different cycles of behavior or hormone regulation such as a breeding, migrating, feeding, molting, or periods of growth (Boily 1996; Boily and Lavigne 1997; Hedd et al. 1997; Nilssen et al. 1997; Beck et al. 2003; Norgarden et al. 2003). External influences can include seasonal changes in the environment such as temperature change, changes in the distribution and amounts of food available, or the ability of an animal to find and assimilate those resources (Boily 1996; Hanel et al. 1996; Domingo-Roura et al. 2001; Anava et al. 2003; Felicetti et al. 2003; Stirrat 2003).

A major difference in the behavior of juvenile and adult southern elephant seals is in their annual haul-out patterns. Only juveniles have a midyear haul-out, whereas the molt is an essential haul-out for all seals. The timing of the haul-outs and physiological processes of the molt haul-out have been described by many authors (Hindell and Burton 1988; Worthy et al. 1992; Boyd et al. 1993; Kirkman et al. 2003). During this time, seals have an increased energy demand and requirement for protein as has been described for other species (Cherel et al. 1988). As they molt, old skin and hair are sloughed and replaced, a process that requires increased blood supply to the skin and increased energy for thermoregulation and protein for cell replacement. The function of the midyear haul-out itself remains unclear (Wheatley 2001; Field et al. 2005), but without the additional costs of molting or breeding, it is likely to be relatively inexpensive.

Seals returned to molt with relatively greater amounts of lean tissue than in the midyear, but they also used more lean tissue during the molt. The metabolism of body reserves is under hormonal control that can mobilize tissues preferentially based on need. As seen in other studies of elephant seals (Biuw 2003; Noren et al. 2003), fatter seals use proportionally more adipose tissue than thinner seals, and fat is catabolized preferentially over protein. Increased rates of protein catabolism may also be required when replacing their epidermis and growing new hair (Robbins 1993). Therefore, it is still unclear whether or how individuals prepare for this additional protein requirement during the previous foraging trip. Individuals may select prey with higher protein content in preparation for this, although it is also possible that this mechanism results from extrinsic factors

such as different prey availability throughout the year (e.g., reduced amounts of prey available in winter).

Sexual Development

Sex differences in body condition and metabolism while ashore have been observed for many species (Winship et al. 2001; Aubret et al. 2002; Beck et al. 2003; Biuw 2003; Field et al. 2002). Differences within adults have been related to the costs of breeding, especially for capital breeders such as elephant seals (Boyd 2002; Beck et al. 2003), where energetic costs for females are typically greater. For juveniles, these differences are related to growth rates and precocious development (Schmidt-Nielsen 1997; Siervogel et al. 2003). We found sex differences in the metabolism of lean and adipose tissue in both the molt and midyear haul-outs, with females tending to metabolize relatively more lean tissue than males. Juvenile males are larger than females (McMahon et al. 1997; Biuw 2003; Field et al. 2002) and grow faster (McLaren 1993); therefore, these differences may be caused by females reaching sexual maturity earlier and at a much smaller size than males. This would allow females to preserve more energy in the form of fat to contribute to upcoming breeding effort. This fat sparing by females supports previous findings by Biuw (2003) where female weanlings had greater fat reserves than males when leaving the beach for their first trip to sea and after subsequent trips. Also, McMahon et al. (1997) showed that most female pups at the time of weaning have all canine teeth whereas all males had not. This supports the observation that females develop earlier and prepare for adulthood in advance of males.

Are Juveniles Energetically Stressed?

While the seals are ashore for both the molt and midyear haul-outs, they fast and use energy reserves. When it is time to return to sea, they must leave the beach with sufficient amounts of both fat and protein to ensure normal thermoregulation and organ function when they resume traveling and foraging. In the past it was thought that seals needed to have a lipid content of more than 10% of total body mass at the end of the haul-out and approximately 70% of the lean body mass (Cahill et al. 1979; Cherel et al. 1987; Reilly 1989) to avoid problems associated with tissue overuse. A recent study by Biuw (2003) has shown that these estimates may be too conservative for juvenile elephant seals embarking on their first trip to sea because many individuals have as little as 50%–60% of their original lean mass (total proteinaceous tissue that could be used). Even during the molt when seals have the greatest protein requirement, they used less than 30% of initial lean tissue and were therefore able to meet their energetic demands without suffering any consequences of overfasting. Before the molt, seals returned with greater proportions of lean to adipose tissue than during the midyear, so it remains unclear whether juveniles are

preparing physiologically for the molt. After the midyear haul-out, juvenile body composition was around 26% adipose tissue compared with 20% during the molt. The reduction in thermal insulation during the molt because of increased peripheral circulation associated with hair growth requires an increased metabolic rate to generate more endogenous heat. These values are higher than the 10% of body mass suggested by Biuw (2003), so juveniles do not appear to be depleting their fat reserves to critical levels. By adapting the use of fat and protein stores to their seasonal demands and environmental temperature variation, juvenile seals demonstrate a remarkable flexibility to maximize resource accumulation.

Our data demonstrate seasonal differences in the energetic requirements and use of lipid and protein stores of juvenile southern elephant seals. Juvenile elephant seals are expending more energy during the molt, older seals have reduced metabolic rates, and there is differential allocation and use of energy by male and females. These differences are most likely related to haul-out function and behavior, growth, and precocious development of females toward sexual maturity. Our use of alternative techniques for the measurement of body composition and metabolic rates demonstrates that the modeling of age-specific energy budgets is possible even without detailed physiological data. However, more information on seasonal and intraspecific differences in the diet, foraging behavior, and growth of juvenile seals will assist our understanding of how elephant seals maximize their energy intake and use.

Acknowledgments

We thank M. Biuw, J. Harrington, F. Jonker, C. McKinley, N. Milius, R. Munro, M. Pauza, and K. Wheatley and members of the 51st–53rd Australian National Antarctic Research Expeditions to Macquarie Island for their assistance during fieldwork. We thank the Australian Antarctic Division for logistic support, especially J. van den Hoff. We also thank M. Biuw, D. Crocker, A. Kabat, J. van den Hoff, and two anonymous reviewers for comments on the manuscript. Funding was provided by the Antarctic Science Advisory Committee and Sea World Research and Rescue Foundation. Data were collected with Australian Antarctic Animal Ethics Committee approval and Tasmanian Parks and Wildlife Service permits.

Literature Cited

- Anava A., M. Kam, A. Shkolnik, and A.A. Degen. 2003. Seasonal field metabolic rate and dietary intake in Arabian babblers (*Turdoides squamiceps*) inhabiting extreme deserts. *Funct Ecol* 14:607–613.
- Arnbom T., M.A. Fedak, I.L. Boyd, and B.J. McConnell. 1993. Variation in weaning mass of pups in relation to maternal mass postweaning fast duration, and weaned pup behaviour in southern elephant seals (*Mirounga leonina*) at South Georgia. *Can J Zool* 71:1772–1781.
- Aubret F., X. Bonnet, R. Shine, and O. Lourdis. 2002. Fat is sexy for females but not males: the influence of body reserves on reproduction in snakes (*Vipera aspis*). *Horm Behav* 42: 135–147.
- Beck C.A., W.D. Bowen, and S.J. Iverson. 2003. Sex differences in the seasonal patterns of energy storage and expenditure in a phocid seal. *J Anim Ecol* 72:280–291.
- Bell C.M., H.R. Burton, and M.A. Hindell. 1997. Growth of southern elephant seals, *Mirounga leonina*, during their first foraging trip. *Aust J Zool* 45:447–458.
- Biuw E.M. 2003. Variations in Body Composition and Energy Utilisation by Southern Elephant Seal Pups over the First Year. PhD thesis, University of St. Andrews.
- Boily P. 1996. Metabolic and hormonal changes during the molt of captive gray seals (*Halichoerus gryphus*). *Am J Physiol* 270: R1051–R1058.
- Boily P. and D.M. Lavigne. 1997. Developmental and seasonal changes in resting metabolic rates of captive female grey seals. *Can J Zool* 75:1781–1789.
- Boness D.J., P.J. Clapham, and S.L. Mesnick. 2002. Life history and reproductive strategies. Pp. 278–324 in A.R. Hoelzel, ed. *Marine Mammal Biology: An Evolutionary Approach*. Blackwell Science, Carlton.
- Boyd I.L. 2002. Energetics: consequences for fitness. Pp. 247–277 in A.R. Hoelzel, ed. *Marine Mammal Biology: An Evolutionary Approach*. Blackwell Science, Carlton.
- Boyd I.L., T. Arnbom, and M.A. Fedak. 1993. Water flux, body composition, and metabolic rate during molt in female southern elephant seals (*Mirounga leonina*). *Physiol Zool* 66: 43–60.
- . 1994. Biomass and energy consumption of the South Georgia stock of southern elephant seals. Pp. 98–120 in B.J. Le Boeuf and R.M. Laws, eds. *Elephant Seals*. University of California Press, Berkeley.
- Boyd I.L., R.M. Bevan, A.J. Woakes, and P.J. Butler. 1999. Heart rate and behavior of fur seals: implications for measurement of field energetics. *Am J Physiol* 276:844–857.
- Brafield A.E. and M.J. Llewellyn. 1982. *Animal Energetics*. Blackie, Glasgow.
- Bryden M.M. 1967. Study of the Biology of the Southern Elephant Seal, *Mirounga leonina* (Linn.): Development and Growth. PhD thesis, University of Sydney.
- Burnham K.P. and D.R. Anderson. 1998. *Model Selection and Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Burton H.R. 1985. Tagging studies of male southern elephant seals (*Mirounga leonina* L.) in the Vestfold Hills area, Antarctica, and some aspects of their behaviour. Pp. 19–30 in J.K. Ling and M.M. Bryden, eds. *Sea Mammals of South Latitudes*. South Australian Museum, Northfield.

- Cahill G.F., E.B. Marliiss, and T.T. Aoki. 1979. Fat and nitrogen metabolism in fasting man. *Horm Metab Res* 2:181–185.
- Carrick R., S.E. Csordas, S. Ingham, and K. Keith. 1962. Studies on the southern elephant seal, *Mirounga leonina* (L.). III. The annual cycle in relation to age and sex. *CSIRO Wildl Res* 7:119–160.
- Cherel Y., J. Leloup, and Y. LeMaho. 1988. Fasting in king penguin. II. Hormonal and metabolic changes during the molt. *Am J Physiol* 254:R178–R184.
- Cherel Y., Y.P. Robin, and Y. LeMaho. 1987. Physiology and biochemistry of longterm fasting in birds. *Can J Zool* 66: 159–166.
- Condy P.R. 1979. Annual cycle of the southern elephant seal *Mirounga leonina* (Linn.) at Marion Island. *S Afr J Zool* 149: 195–219.
- Costa D.P. and T.M. Williams. 1999. Marine mammal energetics. Pp. 176–217 in J.E. Reynolds and S.A. Rommel, eds. *Biology of Marine Mammals*. Melbourne University Press, Melbourne.
- Domingo-Roura X., C. Newman, F. Calafell, and D.W. Macdonald. 2001. Blood biochemistry reflects seasonal nutritional and reproductive constraints in the Eurasian badger (*Meles meles*). *Physiol Biochem Zool* 74:450–460.
- Fedak M.A., T. Arnbohm, and I.L. Boyd. 1996. The relation between size of southern elephant seal mothers, the growth of their pups and the use of maternal energy, fat and protein during lactation. *Physiol Zool* 69:887–911.
- Felicetti L.A., C.T. Robbins, and L.A. Shipley. 2003. Dietary protein content alters energy expenditure and composition of the mass gain in grizzly bears (*Ursus arctos horribilis*). *Physiol Biochem Zool* 76:256–261.
- Field I.C., C.J.A. Bradshaw, H.R. Burton, M.D. Sumner, and M.A. Hindell. 2005. Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals. *Oecologia* 142:127–135.
- Field I.C., C.J.A. Bradshaw, C.R. McMahon, J. Harrington, and H.R. Burton. 2002. Intravenous anaesthesia of elephant seals (*Mirounga leonina*) using tiletamine and zolazepam: effects of age, size, condition and function of haul-out. *Vet Rec* 151: 235–240.
- Hanel R., J. Karjalainen, and W. Weiser. 1996. Growth of swimming muscles and its metabolic cost in larvae whitefish at different temperatures. *J Fish Biol* 48:937–951.
- Hedd A., R. Gales, and D. Renouf. 1997. Inter-annual consistency in the fluctuating energy requirements of captive harp seals *Phoca groenlandica*. *Polar Biol* 18:311–318.
- Hindell M.A. 1991. Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *J Anim Ecol* 60:119–134.
- . 2002. Elephant seals. Pp. 370–373 in W.F. Perrin, B. Wursig, and J.G.M. Thewissen, eds. *Encyclopedia of Marine Mammals*. Academic Press, London.
- Hindell M.A., C.J.A. Bradshaw, M.D. Sumner, K.J. Michael, and H.R. Burton. 2003. Dispersal of female southern elephant seals and their prey consumption during the austral summer: relevance to management and oceanographic zones. *J Appl Ecol* 40:703–715.
- Hindell M.A. and H.R. Burton. 1987. Past and present status of the southern elephant seal (*Mirounga leonina*) at Macquarie Island. *J Zool* 213:365–380.
- . 1988. Seasonal haul-out patterns of the southern elephant seal (*Mirounga leonina* L.) at Macquarie Island. *J Mammal* 69:81–88.
- Hindell M.A., M.A. Lea, M.G. Morrice, and C.R. McMahon. 2000. Metabolic limits on dive duration and swimming speed in the southern elephant seal *Mirounga leonina*. *Physiol Biochem Zool* 73:790–798.
- Hindell M.A. and C.R. McMahon. 2000. Long distance movement of a southern elephant seal (*Mirounga leonina*) from Macquarie Island to Peter 1 Øy. *Mar Mamm Sci* 16:504–507.
- Hindell M.A. and D.J. Slip. 1997. The importance of being fat: maternal expenditure in the southern elephant seal. Pp. 72–77 in M.A. Hindell and C. Kemper, eds. *Marine Mammal Research in the Southern Hemisphere*. Vol. 1. Status, Ecology and Medicine. Surrey Beatty, Sydney.
- Hindell M.A., D.J. Slip, and H.R. Burton. 1994a. Body mass loss of the moulting female southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Polar Biol* 14:275–278.
- . 1994b. Possible causes of the decline of southern elephant seal populations in the southern Pacific and southern Indian Oceans. Pp. 68–84 in B.J. Le Boeuf and R.M. Laws, eds. *Elephant Seals: Population Ecology, Behaviour, and Physiology*. University of California Press, Berkeley.
- Houser D.S. and D.P. Costa. 2001. Protein catabolism in suckling and fasting northern elephant seal pups (*Mirounga angustirostris*). *J Comp Physiol B* 171:635–642.
- Gales N.J. and H.R. Burton. 1987. Ultrasonic measurement of blubber thickness of the southern elephant seal, *Mirounga leonina*, (Linn.). *Aust J Zool* 35:207–217.
- Ihaka R. and R. Gentleman. 1996. R: a language for data analysis and graphics. *J Comput Graphical Stats* 5:299–314.
- Kirkman S.P., M.N. Bester, P.A. Pistorius, G.J.G. Hofmeyr, F.C. Jonker, R. Owen, and N. Strydom. 2003. Variation in the timing of moult in southern elephant seals at Marion Island. *S Afr J Wildl Res* 33:79–84.
- Kirkman S.P., M.N. Bester, P.A. Pistorius, G.J.G. Hofmeyr, R. Owen, and S. Mecenero. 2001. Participation in the winter haulout by southern elephant seals (*Mirounga leonina*). *Antarct Sci* 13:380–384.
- Kleiber M. 1975. *The Fire of Life: An Introduction to Animal Energetics*. Wiley, New York.
- Knox G.A., ed. 1994. *The Biology of the Southern Ocean*. Cambridge University Press, Cambridge.
- Larner J., ed. 1971 *Intermediary Metabolism and Its Regulation*. Prentice-Hall, Englewood Cliffs, NJ.

- Le Boeuf B.J. and R.M. Laws. 1994. *Elephant Seals: Population Ecology, Behaviour, and Physiology*. University of California Press, Berkeley.
- Le Boeuf B.J. and J. Reiter. 1988. Lifetime reproductive success in northern elephant seals. Pp. 344–362 in T.H. Clutton-Brock, ed. *Reproductive Success*. University of Chicago Press, Chicago.
- Lebreton J.-D., K.P. Burnham, J. Clobert, and D.R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118.
- Ling J.K. and M.M. Bryden. 1981. Southern elephant seal *Mirounga leonina* Linnaeus, 1785. Pp. 297–325 in S.H. Ridgway and R.J. Harrison, eds. *Handbook of Marine Mammals*. Vol. 2. Academic Press, London.
- McCann T.S. 1980. Population structure and social organisation of southern elephant seals, *Mirounga leonina* (L.). *Biol J Linn Soc* 14:133–150.
- McConnell B.J., M.A. Fedak, H.R. Burton, G.H. Englehard, and P. Reijnders. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. *J Anim Ecol* 71:65–78.
- McLaren I.A. 1993. Growth in pinnipeds. *Biol Rev Camb Philos Soc* 68:1–79.
- McMahon C.R. 2003. A Demographic Comparison of Two Elephant Seal Populations. PhD thesis, University of Pretoria.
- McMahon C.R., M.N. Bester, H.R. Burton, M.A. Hindell, and C.J.A. Bradshaw. 2004. Population status and trends of a wide-ranging marine mammal predator, the southern elephant seal: re-examining hypotheses to explain the decline. *Mamm Rev* 35:82–100.
- McMahon C.R., H.R. Burton, and M.N. Bester. 2003. A demographic comparison of two southern elephant seals populations. *J Anim Ecol* 72:61–74.
- McMahon C.R., H. Burton, S. McLean, D. Slip, and M. Bester. 2000. Field immobilisation of southern elephant seals with intravenous tiletamine and zolazepam. *Vet Rec* 146:251–254.
- McMahon C.R., J. van den Hoff, H.R. Burton, and P.D. Davis. 1997. Evidence for precocious development in female pups of the southern elephant seal, *Mirounga leonina*, at Macquarie Island. Pp. 92–96 in M.A. Hindell and C. Kemper, eds. *Marine Mammal Research in the Southern Hemisphere*. Vol. 1. Status, Ecology and Medicine. Surrey Beatty, Sydney.
- Mellish J.E., P.A. Tuomi, and M. Horning. 2004. Assessment of ultrasound imaging as a noninvasive measure of blubber thickness in pinnipeds. *J Zoo Wildl Med* 35:116–118.
- Nagy K.A. 2000. Energy costs of growth in neonate reptiles. *Herpetol Monogr* 14:378–387.
- Neumann D.R. 1999. Agonistic behaviour in harbour seals in relation to the availability of haul-out space. *Mar Mamm Sci* 15:507–525.
- Nilssen K.Y., T. Haag, P.E. Grotnes, and V. Potelov. 1997. Seasonal variation in body condition of adult Barent Sea harp seals (*Phoca groenlandica*). *J Northwest Atl Sci Counc* 22: 17–25.
- Noren D.P., D.E. Crocker, T.M. Williams, and D.P. Costa. 2003. Energy reserve utilisation in the northern elephant seal (*Mirounga angustirostris*) pups during the postweaning fast: size does matter. *J Comp Physiol B* 173:443–454.
- Norgarden U., F. Oppedal, G.L. Taranger, G.-I. Hemre, and T. Hansen. 2003. Seasonally changing metabolism in Atlantic salmon (*Salmo salar* L.). I. Growth and feed conversion ratio. *Aquacult Nutr* 9:287–293.
- Ortiz C.L., D.P. Costa, and B.J. Le Boeuf. 1978. Water and energy balance in elephant seal pups under natural fasting conditions. *Physiol Zool* 51:166–178.
- Pace N. and E.N. Rathbun. 1945. Studies on body composition. III. The body water and chemically combined nitrogen content in relation to fat content. *J Biol Chem* 158:685–691.
- Post J.R. and E.A. Parkinson. 2001. Energy allocation strategy in young fish: allometry and survival. *Ecology* 82:1040–1051.
- Reilly J.J. 1989. The water and energy metabolism of grey (*Halichoerus grypus*) and common (*Phoca vitulina*) seals during breeding. PhD thesis, University of Wales College of Cardiff.
- Reilly J.J. and M.A. Fedak. 1990. Measurement of the body-composition of living gray seals by hydrogen isotope-dilution. *J Appl Physiol* 69:885–891.
- Robbins C.T. 1993. *Wildlife Feeding and Nutrition*. 2nd ed. Academic Press, San Diego.
- Schmidt-Nielsen K. 1997. *Animal Physiology: Adaptation and Environment*. 5th ed. Cambridge University Press, Cambridge.
- Siervogel R.M., E.W. Demerath, C. Schubert, K.E. Remsberg, W.C. Chumlea, S. Sun, S.S. Czerwinski, and B. Towne. 2003. Puberty and body composition. *Horm Res* 60:36–45.
- Slip D.J., H.R. Burton, and N.J. Gales. 1992a. Determining blubber mass in the southern elephant seal, *Mirounga leonina*, by ultrasound and isotopic techniques. *Aust J Zool* 40: 143–152.
- Slip D.J., N.J. Gales, and H.R. Burton. 1992b. Body-mass loss, utilization of blubber and fat, and energetic requirements of male southern elephant seals, *Mirounga leonina*, during the moulting fast. *Aust J Zool* 40:235–243.
- Slip D.J., M.A. Hindell, and H.R. Burton. 1994. Diving behaviour of southern elephant seals from Macquarie Island. Pp. 253–270 in B.J. Le Boeuf and R.M. Laws, eds. *Elephant Seals: Population Ecology, Behaviour, and Physiology*. University of California Press, Berkeley.
- Stearns S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stirrat S.C. 2003. Body condition and blood chemistry of Agile Wallabies (*Macropus agilis*) in the wet-dry tropics. *Wildl Res* 30:59–67.
- Webb P.M., D.E. Crocker, S.B. Blackwell, D.P. Costa, and B.J. Le Boeuf. 1998. Effects of buoyancy on the diving behavior of northern elephant seals. *J Exp Biol* 201:2349–2358.

- Wheatley K.E. 2001. Behavioural and Physiological Aspects of the Mid-Year Haul-Out in Southern Elephant Seals (*Mirounga leonina*) on Macquarie Island. MPhil thesis, University of St. Andrews.
- Wieser W. 1994. Cost of growth in cells and organisms: general rules and comparative aspects. *Biol Rev* 69:1–33.
- Winship A.J., A.W. Trites, and D.G. Calkins. 2001. Growth in body size of the stellar sea lion (*Eumetopias jubatus*). *J Mammal* 82:500–519.
- Worthy G.A.J. and D.M. Lavigne. 1983. Energetics of fasting and subsequent growth in weaned harp seal, *Phoca groenlandica*. *Can J Zool* 61:447–456.
- . 1987. Mass loss, metabolic rate, and energy utilization by harp and gray seals pups during the postweaning fast. *Physiol Zool* 60:352–364.
- Worthy G.A.J., P.A. Morris, D.P. Costa, and B.J. Le Boeuf. 1992. Moulting energetic of the northern elephant seal (*Mirounga angustirostris*). *J Zool* 227:257–265.