

Metabolic compensation during high energy output in fasting, lactating grey seals (*Halichoerus grypus*): metabolic ceilings revisited

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Lactation is the most energetically expensive period for female mammals and is associated with some of the highest sustained metabolic rates (SusMR) in vertebrates (reported as total energy throughput). Females typically deal with this energy demand by increasing food intake and the structure of the alimentary tract may act as the central constraint to ceilings on SusMR at about seven times resting or standard metabolic rate (SMR). However, demands of lactation may also be met by using a form of metabolic compensation such as reducing locomotor activities or entering torpor. In some phocid seals, cetaceans and bears, females fast throughout lactation and thus cannot offset the high energetic costs of lactation through increased food intake. We demonstrate that fasting grey seal females sustain, for several weeks, one of the highest total daily energy expenditures (DEE; $7.4 \times \text{SMR}$) reported in mammals, while progressively reducing maintenance metabolic expenditures during lactation through means not explained by reduction in lean body mass or behavioural changes. Simultaneously, the energy exported in milk is progressively increased, associated with increased lipoprotein lipase activity in the mammary gland, resulting in greater offspring growth. Our results suggest that females use compensatory mechanisms to help meet the extraordinary energetic costs of lactation. Additionally, although the concepts of SusMR and ceilings on total DEE may be somewhat different in fasting lactating species, our data on phocid seals demonstrate that metabolic ceilings on milk energy output, in general, are not constrained by the same kind of peripheral limitations as are other energy-consuming tissues. In phocid seals, the high ceilings on DEE during lactation, coupled with metabolic compensation, are undoubtedly important factors enabling shortened lactation.

Keywords: metabolic compensation; energetic ceilings; lactation; phocid seals

1. INTRODUCTION

Lactation is considered the most energetically expensive period for female mammals (Ofstedal 1984; Gittleman & Thompson 1988) and is associated with some of the highest total daily energy expenditures (DEE) and sustained metabolic rates (SusMR) in vertebrates (reported as total energy throughput including milk output) (Kenagy *et al.* 1990; Hammond & Diamond 1992, 1997; Speakman & McQueenie 1996). Females typically, and often exclusively, deal with this energy demand by increasing food intake and it has been proposed that the capacity of the alimentary tract may act as the central constraint to ceilings on DEE and SusMR at about seven times resting or standard metabolic rate (SMR) (Peterson *et al.* 1990; Hammond & Diamond 1992; Speakman & McQueenie 1996; Speakman 1997). (N.B. We use SMR throughout this paper to refer to any metabolic rate measured at rest, including basal metabolic rate (BMR).) However, some species also meet the demands of lactation by exhibiting metabolic compensation (Racey & Speakman 1987), which involves the reduction of expenditure on a component(s) of the energy budget not directly associated with milk production. In small terrestrial animals metabolic compensation is uncommon. Although certain species may reduce locomotor activities (Slonaker

1924; Wang 1924), this usually accounts for only a small fraction of the total energy budget (Racey & Speakman 1987). However, an effective means of metabolic compensation has been demonstrated in bats, which enter torpor (Racey & Speakman 1987), and also in bats and common shrews (*Sorex araneus*) by mechanisms that are not fully understood (Poppitt *et al.* 1993; McClean & Speakman 1999).

A number of studies have attempted to understand the limits to SusMR (or to DEE) and to metabolic outputs in animals experiencing high sustained energy demands. Questions as to whether metabolic ceilings are constrained centrally (i.e. by gut capacity) or peripherally (i.e. by the tissues that use the nutrients), and whether such ceilings are independent of the mode of energy expenditure, are central to understanding organism design and function, patterns of energy allocation during reproduction and the optimization of energy budgets (Ricklefs *et al.* 1996; Speakman 1997; Hammond & Diamond 1997). SusMR has been defined variously as the time-averaged rate of energy use that an animal can support while preserving body mass and energy balance by means of food intake (e.g. Peterson *et al.* 1990), or simply as aerobic metabolism and expenditures that can be sustained for tens of minutes to several hours (Weiner 1989).

In some phocid seals, cetaceans and bears, females fast throughout lactation and thus cannot offset the high

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energetic costs of lactation through increased food intake. They rely instead solely on mobilizing body nutrient stores. The large-bodied phocid seals, family Phocidae, lactate for only 4–50 days (Bowen 1991). Abbreviation of lactation in these species is thought to have evolved in response to the uncertainty associated with giving birth and nursing on unstable ice, as a means of reducing predation and partly as a means of reducing the maternal energetic overhead during lactation (Fedak & Anderson 1982; Stirling 1983). However, the physiological mechanisms contributing to the ability of phocid seals to have shortened lactation periods are not well understood.

The grey seal (*Halichoerus grypus*) is a medium-bodied phocid inhabiting the continental shelves in temperate waters on both sides of the North Atlantic. Females fast throughout their 16-day lactation period and have remarkable rates of milk energy production, secreting up to 4 kg of milk daily that is composed of 40–60% fat (Iverson *et al.* 1993). Because females fast during lactation and pups consume only milk during this time, it is possible to separately measure components of the maternal energy budget using isotope dilution, namely, total DEE, milk energy output (MEO) and maintenance expenditures. Although the grey seal does not maintain mass during lactation, its metabolic output is sustained for several weeks without becoming anaerobic (e.g. Williams 1995). Thus, although SusMR as applied to other species is not strictly comparable to DEE in a fasting lactating animal, we used the grey seal to explore certain aspects of metabolic ceilings during lactation and the potential role of metabolic compensation in the rapid export of energy during lactation.

2. MATERIAL AND METHODS

(a) *Field sampling*

Seventeen grey seal females and their single pups were sampled longitudinally throughout lactation on Sable Island, Canada, in January 1996 and January 1997. Mother–pup pairs were captured on the day of birth (day 0) and placed in a large fenced enclosure (100 m × 100 m) in the middle of the colony, which contained other mother–pup pairs and resident adult males at a density typical of the main breeding colony. Grey seal females on Sable Island use only a small area (about 4 m × 4 m) throughout lactation. Thus the enclosure mimicked their natural setting and allowed aggressive and/or mating encounters with other pairs and adult males, but ensured that we had easy access to the pairs throughout the course of the study. On days 0 ('initial') and 15 ('final') of the approximate 16-day lactation period, females and pups were each weighed to the nearest 0.5 kg and 0.1 kg, respectively. At both these times, females were injected intramuscularly with a weighed dose of tritiated water ($^3\text{H}_2\text{O}$, 5 g of 0.5 mCi ml $^{-1}$) and pups were given a weighed dose of deuterium oxide (D_2O , 99.8 atom%, 3 g kg $^{-1}$) by gastric intubation to determine initial and final total body water (TBW) and thus body tissue and energy changes. After administration, pairs were kept from suckling for 2.5 h to allow the isotope to equilibrate with body fluids, which was confirmed in each animal from serial blood samples. Blood samples were also taken and body mass measured on days 5, 10 and 15 (before re-administration) to determine water flux and milk output (or intake). Milk was collected from each female at these times (0, 5, 10 and 15 days) and analysed for proximate composition

(Mellish *et al.* 1999a). Mammary biopsies were also taken from 11 of the females on the same four sampling days and analysed for lipoprotein lipase (LPL) activity (the primary enzyme responsible for lipid uptake by the mammary gland), by hydrolysis of ^3H -labelled triolein in emulsion (Mellish 1999). All animal-handling procedures conformed to regulations of the Canadian Council of Animal Care.

(b) *Laboratory and data analyses*

Serum samples were distilled and analysed in triplicate for $^3\text{H}_2\text{O}$ and D_2O concentrations according to the methods of Ortiz *et al.* (1978) and Iverson *et al.* (1993), respectively. Initial and final (day 0 and day 15) isotope dilution space was then converted to TBW according to Bowen & Iverson (1998). TBW on days 5 and 10 was determined by interpolation assuming changes in pool size were linearly proportional to mass change in each individual at each sampling point. To measure body tissue and energy changes in both mothers and pups, total body fat and protein were calculated from TBW using the equations derived from grey seal carcass analyses by Reilly & Fedak (1990) and converted to energetic equivalents using the values of 39.3 MJ kg $^{-1}$ and 23.6 MJ kg $^{-1}$, respectively (Blaxter 1989; Iverson *et al.* 1993). The grey seal equations relating TBW to total body energy (Reilly & Fedak 1990) gave the same values. Since females used only body reserves to fuel energy expenditures, their DEEs were calculated from total tissue energy loss divided by days between measurements. Pup daily energy storage was calculated from gains in total tissue energy divided by days between measurements.

Daily milk intake of each pup was calculated as detailed in Oftedal & Iverson (1987) and Iverson *et al.* (1993), using its water (D_2O) turnover, estimated metabolic water production and the average composition of its mother's milk for each time period. Early, mid and late lactation refer to days 0–5, 5–10 and 10–15, respectively. Pup milk intakes were converted to milk energy intakes (MEI) using energetic equivalents (see above, Iverson *et al.* 1993). Since pups suckle only from their mother, pup daily MEI represents their mother's daily MEO. Maintenance metabolic rate (MMR) of mothers and pups refers to the energy required for all daily expenditures other than maternal MEO or pup energy storage, respectively. Thus

$$\text{MMR}_{\text{maternal}} = \text{DEE} - \text{MEO}, \quad (1)$$

$$\text{MMR}_{\text{pup}} = \text{MEI} - \text{energy storage}. \quad (2)$$

Maternal SMR was estimated from averaging the current published data on resting metabolic rates (MJ kg $^{-1}$) measured in adult grey seals ($n=3$, Lavigne *et al.* 1986; $n=3$, Boily & Lavigne 1997) and using a single average (mid-lactation) body mass for each female. Since the majority of maternal mass loss is fat (i.e. about 60% fat, 8% protein; Mellish *et al.* 1999a), the use of a single average SMR for each female seemed appropriate and relied on the fewest assumptions. Given their limited nature, calculations involving estimates of grey seal SMR must be considered tentative. Mammary LPL (U , μmol free fatty acids released per hour per gram of mammary tissue, $n=11$) measured on days 0, 5 and 10 was most representative of early, mid and late periods, respectively; mammary LPL on day 15 reflected termination of lactation in most females and therefore was not included (Mellish 1999).

Rates of maternal mass loss and pup mass gain, and trends in mammary LPL levels over the course of lactation, were tested

Table 1. Mass change and maternal metabolic rates (mean \pm s.e.m.) in 17 lactating grey seal mother-pup pairs

(See §2 for explanation of calculations. Rates of maternal mass loss and pup mass gain are tested by mixed-effects repeated-measures regression (rmANOVA) during lactation.)

	early (0–5 days) <i>n</i> = 17	mid (5–10 days) <i>n</i> = 17	late (10–15 days) <i>n</i> = 16	<i>p</i> (rmANOVA)
maternal mass loss (kg day ⁻¹)	4.2 \pm 0.24	4.0 \pm 0.14	4.3 \pm 0.19	n.s.
pup mass gain (kg day ⁻¹)	1.2 \pm 0.12	1.8 \pm 0.13	2.1 \pm 0.13	< 0.001
maternal DEE (MJ day ⁻¹)	110.1 \pm 8.71	106.0 \pm 6.45	111.0 \pm 4.54	n.s.
milk energy output (MJ day ⁻¹)	44.1 \pm 3.66	63.7 \pm 3.14	74.4 \pm 3.66	< 0.001
maternal MMR (MJ day ⁻¹)	65.9 \pm 8.94	42.3 \pm 6.37	36.6 \pm 3.27	0.004
maternal MMR/SMR	4.5 \pm 0.59	2.9 \pm 0.42	2.5 \pm 0.24	0.004
maternal DEE/SMR	7.5 \pm 0.58	7.3 \pm 0.46	7.5 \pm 0.30	n.s.
mammary LPL (<i>U</i>)	2.5 \pm 0.48	4.6 \pm 0.62	3.9 \pm 0.52	0.051 ^a

^a Mammary LPL levels (*U*, μ mol FFA released per hour per gram of mammary tissue, *n* = 11) increased from early to mid-lactation (*p* = 0.027) but did not differ further during late lactation (rmANOVA, *p* = 0.051 overall). Only early and late periods are tested for the remaining components by rmANOVA, due to a shared reliance on intermediate body composition values in calculations.

using mixed-effects, repeated-measures regression models (S-plus v. 4.0, MathSoft Inc., Seattle, WA, USA). Only early and late rates for the remaining components were tested statistically by repeated-measures ANOVA, due to a shared reliance of the mid-lactation calculations on intermediate body composition values. Data are presented as means \pm s.e.m.

3. RESULTS

(a) Maternal energy budgets and allocation

The females used in our study ranged from 138.0 to 234.0 kg (mean 196.4 \pm 6.36 kg) at parturition and rates of mass loss were constant over the course of lactation at about 4.2 kg day⁻¹ (table 1). Consistent with a linear mass loss, maternal DEE did not change during lactation, averaging 108.4 \pm 5.08 MJ day⁻¹ over all periods. However, the allocation of that daily energy budget shifted dramatically (figure 1). In early lactation, maternal MMR averaged 66 MJ day⁻¹ and accounted for the majority (57.3 \pm 3.47%) of total DEE. However, by mid and late lactation, maternal MMR had decreased by 36% and 45%, respectively (table 1). Thus, although DEE remained unchanged, MMR accounted for only 37.3 \pm 3.98% and 32.4 \pm 2.79% of DEE by mid and late lactation, respectively (figure 1). Although female grey seals fuel > 91% of energy expenditures using stored fat (Mellish *et al.* 1999a), lean body mass (LBM) decreased from 129.0 \pm 4.27 kg LBM (early) to 113.4 \pm 4.45 kg LBM (late) or by 12%. However, MMR expressed as a function of LBM still decreased by 38% from early to late lactation (*p* = 0.016), averaging 0.52 \pm 0.073, 0.36 \pm 0.052 and 0.32 \pm 0.034 MJ kg LBM⁻¹ day⁻¹ during early, mid and late periods, respectively. Thus, the majority of the decrease in observed MMR could not be accounted for by the decrease in LBM.

During the same periods that MMR decreased, maternal MEO increased by 44% and 69%, respectively (table 1). This increase in MEO was associated with a 56–84% increase in mammary LPL activity from early to mid and late lactation (table 1). We estimated that the SMR of our females averaged 14.7 \pm 0.39 MJ day⁻¹. Hence maternal DEE represented a relatively constant

average of 7.4 \pm 0.35 \times SMR throughout all lactation periods, while MMR declined significantly from 4.5 \times SMR (early) to 2.5 \times SMR (late) (table 1).

(b) Pup energy use and allocation

The birth mass of the pups of these females ranged from 12.5 to 19.5 kg (16.5 \pm 0.51 kg). Consistent with increased rates of maternal MEO (i.e. pup MEI) as lactation progressed, pup mass gain was significantly greater in the mid and late stages of lactation (table 1). Although absolute pup MMR increased from 14.5 \pm 0.86 MJ day⁻¹ (early) to 18.0 \pm 1.09 MJ day⁻¹ (mid) and 23.0 \pm 2.18 MJ day⁻¹ (late) (*p* = 0.001), it did so proportionately with increases in LBM. Pup MMR expressed as a function of LBM did not differ throughout (*p* > 0.3), averaging 0.86 \pm 0.039, 0.91 \pm 0.056 and 0.96 \pm 0.081 MJ kg LBM⁻¹ day⁻¹ during early, mid and late periods, respectively. Additionally, the relative allocation of pups' total daily energy budget to MMR remained constant (*p* > 0.3), averaging 29.8 \pm 1.68% throughout (figure 1). However, the increased MEO in mid to late lactation resulted in 54–73% greater pup energy storage (from 29.7 \pm 3.43 MJ day⁻¹ (early) to 45.7 \pm 2.81 MJ day⁻¹ (mid) and 51.4 \pm 3.28 MJ day⁻¹ (late), figure 1) and 50–75% greater rates of mass gain (primarily fat) compared to early lactation (table 1).

4. DISCUSSION

Female grey seals on Sable Island achieve rapid rates of energy transfer to their pups through the production of large volumes of high-fat milk during a brief 16-day lactation period (Iverson *et al.* 1993). The magnitude of this energy flow in females was reflected in an overall DEE of 7.4 \times SMR estimated for grey seals (Lavigne *et al.* 1986; Boily & Lavigne 1997) (table 1) or 8.1 \times predicted SMR (or BMR) from Kleiber's equation (Kleiber 1975). Northern elephant seal (*Mirounga angustirostris*) females also fast throughout lactation (26 days), and although twice the size at parturition, have a lower mass-specific DEE (0.34 MJ day⁻¹ kg) than grey seal females (0.66 MJ day⁻¹ kg) and correspondingly lower estimates

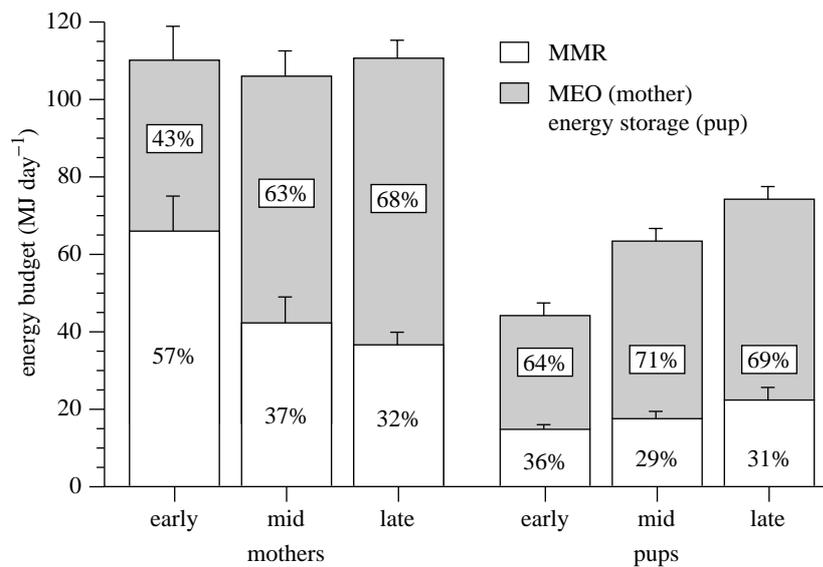


Figure 1. Changes in energy allocation in 17 grey seal mother-pup pairs over lactation. Early, mid and late lactation refer to days 0–5, 5–10 and 10–15, respectively. See text for explanation of measurements and calculations. Bars represent absolute values (MJ day^{-1}). Numbers within bars represent the average relative proportions (calculated from each individual) allocated to MMR versus MEO in mothers or energy storage in pups. Maternal DEE remained constant ($p > 0.9$), while allocation (percentage of energy budget) to MMR decreased ($p < 0.001$), resulting in increased allocation to MEO over lactation ($p < 0.001$); pup energy allocation to MMR versus storage did not change ($p > 0.3$, rmANOVA).

of DEE relative to Kleiber's predicted SMR ($5.4\text{--}6.0 \times \text{SMR}$) (Costa *et al.* 1986).

There are three primary means by which animals can deal with an increased energy demand such as lactation. As previously mentioned, the first and most common response is to increase food consumption. Energy intake during lactation can increase up to fivefold in some species (reviewed in Gittleman & Thompson 1988). A second way that animals can deal with increased energy demand is to mobilize body energy stores, typically to augment increases in food intake. Because they fast, grey seal females rely solely on body energy reserves to supply both maintenance needs and those of milk synthesis, depleting up to 36% of their initial body mass and 57% of their initial energy reserves by the end of lactation (Fedak & Anderson 1982; Reilly *et al.* 1996; Mellish *et al.* 1999a). A third mechanism, known as metabolic compensation, involves the reduction of expenditure on non-lactational components of the energy budget. Evidence for compensation has been found in rodents through decreased activity (Slonaker 1924; Wang 1924) or reduced brown adipose tissue thermogenesis (Trayhurn *et al.* 1982; Trayhurn 1983), and in bats, marsupials and monotremes by entering torpor (Racey & Speakman 1987; Geiser & Masters 1994). There have also been reports of increased metabolic efficiency in lactating humans (Illingworth *et al.* 1986), rodents and insectivores (e.g. Trayhurn *et al.* 1982; Poppitt *et al.* 1993), but none of the magnitude shown by the females in this study.

We were able to divide components of the maternal energy budget of grey seals into the costs directly incurred as milk export versus the costs of maintenance expenditures (MMR). Intuitively, any reduction in components of MMR would be beneficial to a fasting, lactating animal, such as the grey seal, experiencing such high levels of DEE. In fasting-adapted species one might

expect to see metabolic depression through means such as hibernation, torpor or reduced activity (Guppy *et al.* 1994). However, sustained metabolic compensation during lactation has not previously been documented in a fasting animal that remains active. Despite a constant high DEE throughout lactation, by mid and late periods both absolute MMR and the fraction of DEE allocated to MMR decreased by almost one-half, with a corresponding increase in energy devoted to MEO (figure 1), suggesting that females progressively invoked some form of metabolic compensation.

Maintenance expenditures of lactating females depend on basal metabolism (i.e. body size), thermoregulatory costs, activity costs, additional heat losses incurred with milk production and specific dynamic action if feeding. Increases in basal or standard metabolism are expected in lactating animals (Canas *et al.* 1982; Thompson 1993) and were evident in grey seal females at an average MMR of about $3.4 \times$ estimated SMR. In fact, increases in milk production should further increase heat loss through the inefficiencies of converting dietary or stored energy into milk (Romero *et al.* 1976; Baldwin *et al.* 1980; Rogowitz 1998). Hence, the 44–69% greater milk energy production during the later stages of lactation in grey seals would actually be expected to be associated with an increase in MMR, rather than the observed 45% decrease.

Changes in the behaviour or LBM of grey seal females can account for neither the magnitude of change in MMR between early and mid or late lactation nor the continued reduction of maternal MMR in late lactation. Although lactating grey seals spend the majority of time (60%) idle or resting throughout lactation, during later stages of lactation females actually increase their activity through more frequent aggressive and/or mating interactions with adult males (Boness *et al.* 1995; Haller *et al.*

1996). This was evident in our females as well, as all had increased social interactions with other females and with adult males during the mid to late periods (also see §2). It is possible that while activity increased over lactation, the energy expended during that activity could have decreased with the decrease in body mass of females. However, the extent to which this might have contributed to the reduction observed in MMR is not possible to assess with our data. Finally, although reduction of LBM might have caused a commensurate decrease in metabolism, 84–86% of the observed decline in MMR was still unexplained after accounting for LBM changes. Thus, while an obvious source for the reduction of the maintenance component was not apparent, metabolic compensation appears to be an important factor in the ability of females to maximize energy transfer to their pups while fasting.

Most feeding mammals can maintain SusMR of only 2–4 × SMR and generally measurements have not exceeded 6.9 × SMR (reviewed in Peterson *et al.* 1990; Hammond & Diamond 1997). The highest DEE or SusMR (7.2 × SMR) have been reported in lactating rodents (Kenagy *et al.* 1990; Hammond & Diamond 1992). These studies have led to the view that 7 × SMR may represent a metabolic ceiling for extended periods of expenditure, including lactation (Hammond & Diamond 1992; Speakman 1997). A central question to understanding these apparent metabolic ceilings is whether they are constrained either centrally (by the energy-supplying machinery, i.e. the gut) or peripherally (by the energy-consuming machinery, i.e. effector organs) (Weiner 1989; Peterson *et al.* 1990; Hammond *et al.* 1996; Hammond & Diamond 1997). To date, data on metabolic ceilings in lactating animals have been based on fed animals, which can and must largely compensate for increased expenditure through increases in food consumption. Hence the clear separation of central versus peripheral limitations has been difficult to assess. Only some large phocid seals, cetaceans and bears can successfully complete lactation while fasting. Thus, any limits to DEE during lactation cannot be imposed centrally by the capacities of the gut. Additionally, ceilings on DEE may be somewhat different in animals that have incurred the metabolic costs of digestion and assimilation of food energy prior to lactation versus those that incur them simultaneously with lactation. The high DEE in grey seals (7.4 × SMR) is consistent with this expectation. Furthermore, DEE can clearly reach even higher levels. In the similarly sized hooded seal (*Cystophora cristata*), which lactates for only four days, DEE is about 216 MJ day⁻¹ or 11.8 estimated SMR (figure 2; Mellish *et al.* 1999b). Nevertheless, we propose that SusMR as previously reported in lactating mammals (i.e. as DEE, Kenagy *et al.* 1990; Hammond & Diamond 1992, 1997; Speakman & McQueenie 1996) is different from SusMR measured for other types of activities. Rather, it represents SusMR plus an energy export term. Furthermore, while SusMR may be constrained by a maternal metabolic ceiling, the export term is not likely to be constrained in the same way, as we describe below.

During lactation, the SusMR of females due to muscular work and heat production (i.e. fuel catabolism) is represented by MMR. In female grey seals MMR was

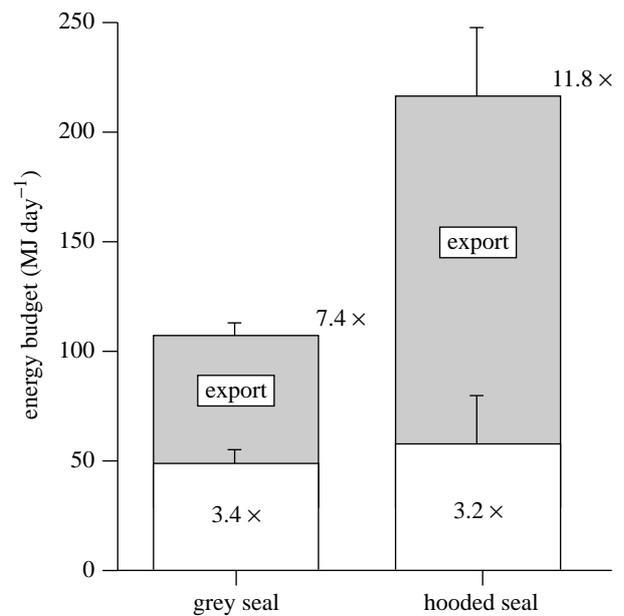


Figure 2. DEE and allocation of the daily energy budget to export (filled bars) versus maintenance (open bars), relative to estimated SMR, in grey seals and hooded seals averaged across their full lactation periods (16 days and four days, respectively). Data for hooded seals ($n = 6$) derived from Mellish *et al.* (1999b).

estimated to be about 2.5–4.5 × SMR (table 1). This MMR (averaging 3.4 × SMR) is remarkably similar to that estimated for similarly sized lactating hooded seals at 3.2 × SMR (figure 2). The remainder of DEE (i.e. MEO) represents the rapid mobilization and export, but not catabolism, of maternal body stores. In females of non-ruminant species that feed and maintain body mass during lactation, the digested dietary energy that is exported in milk is also not catabolized for tissue demands: it is simply restructured and exported, especially in carnivores (Iverson 1993). That is, costs associated with milk production in carnivores and many omnivores will not be incurred from lipid or fatty-acid synthesis, but rather from lipid turnover or resynthesis (i.e. reforming of triacylglycerols from dietary or stored fatty acids directly entering the mammary gland). Similarly, milk proteins are also derived mostly from resynthesis (i.e. reassembling into milk proteins the dietary or stored amino acids entering the mammary gland). These turnover costs are likely to be comparatively low and relatively efficient (Milligan 1971; Baldwin & Smith 1974; Baldwin *et al.* 1980). Thus, while energy expenditure by muscles for exercise may be constrained by the muscle's ability to both uptake and catabolize nutrients (Peterson *et al.* 1990), the energy exported in milk is not, in fact, limited by tissue catabolism. Hence the ceiling for sustained DEE (i.e. MMR + MEO) during lactation should be much higher than for other types of energy expenditure, as we have demonstrated for phocid seals.

In grey seals, a combination of mammary gland capacity (e.g. size, metabolic activity), nutrient availability and metabolic compensation appear to maximize the capacity for MEO. Fatty acids from extensive blubber stores provide the main energy source in milk and are

transferred directly, unmodified, from blubber into milk (Iverson *et al.* 1995b). Thus, uptake of fatty acids by the mammary gland will be a primary constraint on daily MEO. Circulating fatty acids are carried primarily as triacylglycerols (Iverson *et al.* 1995a) and require the activity of mammary LPL to be taken up by the mammary gland. In grey seal females, mammary LPL activity increased by an average of 70% over lactation (table 1), coupled with increased milk lipid and energy output (figure 1). Thus, increased mammary capacity appears to underlie increased energy export, which has also been demonstrated for mice (Hammond *et al.* 1996) and hooded seals (Mellish *et al.* 1999b).

It has been suggested that high energy budgets or SusMR might be constrained by requiring disproportionately high increases in supporting metabolic machinery (Hammond & Diamond 1997). However, similar levels of MMR in grey seals and hooded seals, despite very large differences in the levels of DEE and MEO (figure 2), suggest that this is not necessarily the case with high mammary outputs. Also, MEO increased in grey seals over lactation while MMR did not increase, further supporting the notion that mammary gland outputs are not constrained in the same way as other energy-supplying organs. Independence of milk output and maintenance expenditure, rather than a competitive allocation of these components, has been indicated previously in cotton rats (*Sigmodon hispidus*) (Rogowitz 1998). However, our data suggest that there are trade-offs in the allocation of energy during lactation in grey seals. This is unexpected in that the processes and constraints acting on the two types of activities are likely to be quite different. As stated above, MMR will depend upon body size, thermoregulation and activity levels, while milk production should depend more on mammary capacity, nutrient availability and neonatal suckling intensity (Hammond *et al.* 1996; Rogowitz 1998; Mellish *et al.* 1999b). These contrasting findings raise the possibility that the way in which animals deal with metabolic ceilings on MMR and MEO, and the relative allocation to these, may differ according to life-history patterns. In phocid seals, the high ceilings for DEE during lactation, coupled with metabolic compensation, are undoubtedly important factors enabling shortened lactation.

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