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Use of maternal reserves as a lactation strategy in large mammals

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The substrate demands of lactation must be met by increased dietary intake or by mobilization of nutrients from tissues. The capacity of animals to rely on stored nutrients depends to a large extent on body size; large animals have greater stores, relative to the demands of lactation, than do small animals. The substrate demands of lactation depend on the composition and amount of milk produced. Animals that fast or feed little during lactation are expected to produce milks low in sugar but high in fat, in order to minimize needs for gluconeogenesis while sustaining energy transfers to the young. The patterns of nutrient transfer are reviewed for four taxonomic groups that fast during part of or throughout lactation: sea lions and fur seals (Carnivora: Otariidae), bears (Carnivora: Ursidae), true seals (Carnivora: Phocidae) and baleen whales (Cetacea: Mysticeti). All these groups produce low-sugar high-fat milks, although the length of lactation, rate of milk production and growth of the young are variable. Milk protein concentrations also tend to be low, if considered in relation to milk energy content. Maternal reserves are heavily exploited for milk production in these taxa. The amounts of lipid transferred to the young represent about one-fifth to one-third of maternal lipid stores; the relative amount of the gross energy of the body transferred in the milk is similar. Some seals and bears also transfer up to 16–18 % of the maternal body protein via milk. Reliance on maternal reserves has allowed some large mammals to give birth and lactate at sites and times far removed from food resources.

Lactation: Fasting: Milk composition: Seals: Bears: Whales

Lactation involves the mobilization and export of substantial quantities of nutrients in milk, placing large nutrient demands on the mother. If she is unable to meet these added demands by dietary intake, she must reduce milk output, mobilize nutrients from maternal tissues or employ some combination thereof. However, reduction in milk output may compromise survival of the young. In nature, lactation is often timed to periods of food abundance so that the mother can match dietary intake to lactational needs, and does not have to choose between her own future and that of her offspring.

An alternative approach is to disengage lactation from maternal food intake by storing nutrients in tissues during periods of abundance and then mobilizing these nutrients into milk at a later date. Such an approach is only possible if the types and amounts of nutrients stored in tissues are

sufficient to cover the demands of lactation. The sufficiency of nutrient storage is largely governed by the allometry of energy expenditure (Oftedal, 1993): since small animals expend energy at a much higher rate (relative to body mass) than large animals, small animals are physically unable to store sufficient energy to cover expenditures for any length of time.

A simple calculation for 4 g shrews illustrates this point. If a shrew deposits body fat equivalent to 250 mg/g body mass (M), the energy content of the fat stores will be about 39 kJ, while lean tissue will contain approximately 16 kJ. If the shrew can mobilize stored reserves into milk energy with an efficiency of 84 % (Agricultural Research Council, 1980), and if it can transfer one-third of its stored reserves into milk and survive (see p. 104), the shrew can theoretically cover a milk energy output of 15 kJ from maternal

Abbreviation: M, body mass.

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reserves. However, daily milk energy outputs are much higher than this value. Masked shrews (*Sorex cinereus*; adult weight 3.9 g) rear litters of about six young, each weighing about 3.5 g at peak lactation (Forsyth, 1976). A litter of this metabolic mass would require about 52 kJ in milk per d (Oftedal, 1984). Thus, a masked shrew can only cover a small proportion of its daily milk energy output, even if it mobilizes one-third or more of its stored reserves.

In the present paper I will examine some of the factors that facilitate dependence on stored reserves, and give examples of lactation strategies in which reliance on stored nutrients is essential, because females are lactating while fasting.

The impact of body mass in large mammals

The amount of energy required for milk output will depend on production level, while the amount available will depend on the magnitude of energy stores that can be mobilized. As energy storage is proportional to $M^{1.0}$ and milk energy output is proportional to metabolic body size ($M^{0.75}$; Linzell, 1972; Oftedal, 1984), energy stores:energy demand is proportional to $M^{1.0}/M^{0.75}$, i.e. $M^{0.25}$. A species that is ten times larger than another should have $10^{0.25}$ i.e. 1.78 times larger energy reserves, relative to milk energy output. This calculation assumes that there are no species-specific differences in body fat storage, and that the lactation curves of the species are similar, as one would expect if the species had similar reproductive patterns (Oftedal, 1984).

The effect of body size can be illustrated by a comparison among ungulates (orders Artiodactyla, Perissodactyla and Proboscidea). At peak lactation inter-species differences in energy output in milk (EO_{PL}) are dependent on M (kg): EO_{PL} (MJ/d) = $0.44M^{0.70}$ (Oftedal, 1985). If expressed relative to maternal metabolic size ($M^{0.75}$), peak energy outputs in ungulates range from 0.19 to 0.59 MJ/kg $M^{0.75}$ per d, a range similar to that of metabolizable energy requirements for maintenance, 0.3–0.6 MJ/kg $M^{0.75}$ per d (Hudson & Christopherson, 1985; Oftedal, 1985; Carl & Robbins, 1988; Reese & Robbins, 1994). The energy content of the body may be estimated approximately on the assumption that fat content does not exceed about 250 g/kg, and that lean mass contains 220 g protein/kg (Agricultural Research Council, 1980); energy content of the body will then be about 14 MJ/kg, regardless of body size. Assuming 84 % efficiency in converting stored energy to milk energy (Agricultural Research Council, 1980), and that one-third of stores can be mobilized into milk, the period of lactation that could be supported in theory from stores is about 14 d in a very small ungulate such as the 4.5 kg dik-dik (*Madoqua kirki*), but about 94 d in a very large one such as a 2700 kg elephant (*Elephas maximus*). Estimates for intermediate sizes include 28 d for a 50 kg mule deer (*Odocoileus hemionus*), 47 d for a 270 kg plains zebra (*Equus burchelli*), and 69 d for a 950 kg giraffe (*Giraffa camelopardalis*). These values represent maxima, assuming the females are fat and that they obtain sufficient energy from food to cover maintenance needs and only have to use stored reserves for milk production. They undoubtedly overestimate energy storage for many species. In many ungulates birth occurs at the beginning of the spring or monsoon flush of plant

growth, at a time when the mothers have relatively little body fat (White & Luick, 1984).

The effects of size on nutrient reserves complicate inter-species comparisons, especially when a smaller species (such as a mouse or rat) is used as a model for a larger species (such as man). Nutritional deficiency tends to develop more quickly in the small species. The ability of very large animals to buffer short-term deficits in nutrient availability by reliance on stored reserves may have provided an evolutionary advantage for large-bodied 'megaherbivores' such as elephants and rhinoceros. During the Pliocene and Pleistocene periods megaherbivores were more abundant than they are today, being represented by twenty-one to twenty-eight genera rather than the eight genera that now survive (Owen-Smith, 1988).

Substrates for milk secretion

The foregoing discussion ignores the fact that substrates required for milk synthesis are not interchangeable. Mammary glands are unable to synthesize essential amino acids or long-chain polyunsaturated fatty acids de novo, and must have additional sources of non-essential amino acids for amino acid and protein synthesis, glucose or glucose precursors for lactose and oligosaccharide synthesis and, depending on species, fatty acids, ketone bodies, acetate and/or glucose for triacylglycerol synthesis (Linzell, 1968; Williamson *et al.* 1995; Bell & Bauman, 1997; Vernon & Pond, 1997; Shennan, 1998). The amounts of particular substrates required by the mammary glands will depend primarily on the amount and composition of milk produced, and secondarily on taxon-specific peculiarities of the biosynthetic pathways of mammary secretory cells. For example, the absence of citrate lyase from the cytosol of ruminant mammary cells restricts use of glucose as a substrate for fatty acid synthesis. This factor serves to conserve limited glucose supplies in animals in which little carbohydrate enters the blood circulation from the digestive tract as a consequence of rumen fermentation. Even without glucose use for fatty acid synthesis, ruminant mammary glands co-opt a large proportion of the glucose produced by hepatic gluconeogenesis, since so much glucose is needed to produce relatively lactose-rich milks (Bell & Bauman, 1997).

Mammals produce milks that differ greatly in composition among taxa, with fat varying from less than 10 g/kg (in rhinos, some lemurs) to more than 600 g/kg (in some seals), and carbohydrate from trace amounts (in sea lions and fur seals) to 130 g/kg (in some marsupials) (Oftedal & Iverson, 1995). Evolution has clearly altered the substrate demands of mammary glands by alteration of milk composition. When coupled with the substantial taxonomic variation in lactation intensity, as reflected in litter size, peak energy output and lactation length (Oftedal, 1984), mammary glands pose greatly different demands on the body in different mammals. For example, at peak lactation horses (515 kg) produce 17.6 kg milk containing 0.22 kg fat and 1.2 kg carbohydrate, whereas hooded seals (*Cystophora cristata*; 179 kg) produce 7.5 kg milk containing 4.5 kg fat and 0.08 kg carbohydrate (Oftedal *et al.* 1983, 1993b). Daily fat output represents 2.5 % maternal M in hooded seals, but

only 0.04 % in horses, while daily carbohydrate output represents 0.23 % maternal M in horses, but only 0.04 % maternal M in hooded seals.

Lactation during fasting: some examples

The need to draw on stored reserves to support lactation is most evident when food intake is negligible. A two- to threefold increase in food intake occurs during lactation in many domestic and laboratory animals, such as the mouse (Hammond & Diamond, 1994), rat (Cripps & Williams, 1975) and cat (Loveridge, 1986). Yet some mammals, such as seals, bears and baleen whales, rely entirely on stored substrate precursors for part of or throughout lactation. Each of these species must integrate the substrate requirements of the mammary glands into the suite of substrate-sparing metabolic changes associated with fasting. Fasting animals face a long-term shortage of glucogenic precursors due to the limited amounts of glycogen stored in the body, the fact that only modest amounts of glycerol become available from lipolysis, and the need to conserve glucogenic amino acids. A number of the characteristic metabolic adjustments to fasting, such as increased production and use of ketone bodies, reductions in glucose use by peripheral tissues, and changes in insulin sensitivity, are part of an overall strategy of minimizing glucose use and thereby sparing amino acids, and hence tissue proteins, for other vital functions.

Mammals that lactate while fasting must minimize glucose use or face rapid and debilitating loss of tissue proteins as the C skeletons of glucogenic amino acids are diverted to glucose synthesis. It is unlikely that any mammal producing milk high in lactose and oligosaccharides, such as the 60–80 g total sugars/kg in equid or anthropoid primate milks (Oftedal & Iverson, 1995), could fast for more than a brief period and sustain lactation. One would expect all mammals that routinely fast during lactation to produce milks very low in sugar content. The primary source of energy must therefore be fat. High-fat milks also contain relatively little water on a per kJ basis, which may be of particular benefit for species that do not drink during lactation and must derive all milk water from body fluids and from catabolic processes.

One would also expect that fasting mothers could conserve tissue protein by producing low-protein milk, but this process is only feasible if the offspring have low protein requirements due to a slow rate of growth. However, a slow rate of growth implies a longer period of dependence, which may be too energetically demanding for the mother if she continues to fast. A slow rate of growth may be appropriate for species in which fasting is intermittent or covers only a portion of lactation, but if the entire lactation is to be completed while fasting, growth should be rapid to allow early weaning and maternal resumption of feeding.

The solutions adopted by different mammals vary. The remainder of the present paper briefly summarizes the patterns of substrate mobilization from maternal reserves in four taxa that fast during lactation. Space does not permit a comprehensive review of lactation patterns of these groups, but recent reviews are available (Oftedal *et al.* 1987a; Costa, 1991; Oftedal, 1993, 1997; Boness & Bowen, 1996). The discussion is limited to the major constituents of milk,

although the massive mobilizations into milk of other specific constituents, such as amino acids, electrolytes, Ca, P and vitamins, also pose significant demands on the fasting animal. In these species the fatty acid composition of the milk is a close reflection of the fatty acid composition of adipose tissue triacylglycerols (Iverson & Oftedal, 1992; Iverson *et al.* 1995).

Sea lions and fur seals (*Carnivora: Otariidae*)

All species of the family Otariidae appear to follow a similar lactation pattern: mothers come ashore to give birth, remain ashore for an initial 5–9 d perinatal period, and then begin a cycle of foraging at sea alternating with nursing pups on shore (Oftedal *et al.* 1987a; Boness & Bowen, 1996). The ‘at sea’ phase lasts about 1–12 d and the ‘on shore’ phase 1–5 d, depending on species; the lactation period encompasses 4–12 or more months, again depending on species. Since otariid females cannot feed while on shore, the lactation period includes an initial fast and subsequent fast periods. California sea lions (*Zalophus californianus*) and northern fur seals (*Callorhinus ursinus*) are presumably typical of otariids in producing milks devoid of lactose, and containing but trace amounts (<6 g/kg) of other carbohydrates; otariid milks are also high (250–500 g/kg) in fat (Pilson & Kelly, 1962; Johnson, 1975; Dosako *et al.* 1983; Oftedal *et al.* 1987a, b; Kretzmann *et al.* 1991; Arnould & Boyd, 1995a). The percentage of energy supplied by protein is quite low (12–21) by comparison with carnivores that do not fast during lactation (27–50; Gittleman & Oftedal, 1987). This low level is believed to reflect the slow rates of growth and relatively high energy expenditure rates of sucking pups (Oftedal *et al.* 1987b; Thompson *et al.* 1987). The composition of the milk thus conforms to expectations for a fasting animal.

The extent of mobilization of energy, fat and protein can be estimated for the Antarctic fur seal (*Arctocephalus gazella*) on the basis of data on female M, body composition, milk production and milk composition (Arnould & Boyd, 1995; Arnould *et al.* 1996a,b; Arnould, 1997). During the 6 d perinatal period, a 40 kg female produces nearly 3 kg milk containing about 53 MJ energy, 1.1 kg fat and 0.3 kg protein. Assuming that the parturient female contains 146 g fat/kg and 211 g protein/kg, as do females later in lactation (Arnould *et al.* 1996b), she transfers about 12 % body energy, 19 % body fat and 4 % body protein into milk during the postnatal fast.

Nutrients are also mobilized from body stores during subsequent ‘on shore’ periods, but the amounts involved are more difficult to estimate. When the Antarctic fur seal mother returns after foraging at sea for 2–8 d, she carries newly acquired nutrients stored in adipose and other non-mammary tissues as well as milk in the mammary glands. In otariids, the mammary glands are apparently capacious: they spread like an extensive apron over the abdomen, lower thorax and sides of the body (Scheffer, 1962). Based on milk expression, Arnould & Boyd (1995b) estimated that females bring ashore about 1.2 kg milk. Given that total milk yield during ‘on shore’ periods averages 3.4 kg (Arnould *et al.* 1996a), the amount of milk synthesized from maternal reserves is about 2.2 kg, containing about 39 MJ energy,

0.89 kg fat and 0.23 kg protein. These levels are lower than those during the perinatal period, but are nonetheless substantial.

The bears (Carnivora: Ursidae)

Relatively little is known about tropical and subtropical bears, but the temperate and arctic species such as black bears (*Ursus americanus*), brown bears (*Ursus arctos*) and polar bears (*Ursus maritimus*) are known to give birth in a rock den, snow den or brush pile during winter when they are dormant or 'hibernating'. The mothers remain in this state for the first 2–3 months postpartum, and do not emerge to eat or drink despite the fact that they are lactating. As the females are also confined to the den for 1 or more months before parturition, the total length of the fast is typically 4–5 months in black and brown bears, but may be as much as 8 months in polar bears in areas that are unsuitable for hunting during late summer and autumn due to melting of the sea ice (Atkinson & Ramsay, 1995). Lactation persists for 11 or more months.

The demands of lactation are reduced by the small size of the young (about 0.3 % maternal M at birth) and by the fact that the mothers ingest the excreta of the cubs, thereby recovering water and possibly N that had been secreted in the milk (Ramsay & Dunbrack, 1986; Oftedal *et al.* 1993a). The high fat (150–350 g/kg, depending on stage and species) and low sugar (10–30 g/kg) concentrations of bear milks (Jenness *et al.* 1972; Ando *et al.* 1979; Derocher *et al.* 1993; Oftedal *et al.* 1993a; Farley & Robbins, 1995) are thought to be adaptations to the constraints of fasting metabolism, as is the relatively small percentage of energy provided by protein (15–19; Gittleman & Oftedal, 1987; Oftedal, 1993). Bear milks contain only trace amounts of lactose; the bulk of the sugar is comprised of oligosaccharides (Urashima *et al.* 1997).

The giant panda (*Ailuropoda melanoleuca*) provides an intriguing contrast to bears as it is of similar size, is closely related and produces very small neonates, but does not fast for more than a few days after birth. Giant panda milk is quite similar in fat (184 g/kg) and sugar (27 g/kg) content to the milks of black and brown bears, but the protein level is higher (83 g/kg or 22 % gross energy; Pan *et al.* 1998). Whether this difference is due to relaxation of the constraints posed by fasting, or a reflection of elevated protein needs of the young, or both, is not known.

The demands of lactation in fasting bears can be estimated in black and brown bears; the only data available on milk production in polar bears are for females with older cubs (Arnould & Ramsay, 1994). In the first 3 months of fasting black bear mothers provide each cub about 11 kg milk containing 2.7 kg fat, 0.81 kg protein and 0.27 kg sugar (Oftedal *et al.* 1993a). A 97 kg lactating bear rearing triplets produces about 34 kg milk, equivalent to 35 % maternal M. The large mammary demand for fat is met by lipids stored before parturition; at birth the female contains about 400 g body fat/kg (Oftedal, 1993; Atkinson & Ramsay, 1995; Hilderbrand *et al.* 1998). During the first 3 months the black bear with triplets invests about 21 % maternal body fat, 19 % maternal body protein and 21 % maternal body gross energy into the synthesis of milk constituents. Investment by

brown bears (161 kg) is similar or greater. In the first 2 months of hibernation, lactating brown bears secreted more fat, protein and sugar (equivalent to 4.8, 2.0 and 1.0 % maternal M respectively) than black bears (3.4, 1.1 and 0.4 % maternal M respectively), even though both species were rearing twins (Farley & Robbins, 1995). Whether brown bears typically invest a greater proportion of maternal reserves than black bears may depend on such factors as maternal body composition at birth, litter size, time of emergence from the den, and availability of food after den emergence.

The true seals (Carnivora: Phocidae)

The true seals or phocids all haul themselves onto a solid substrate, either land or ice, to give birth and nurse their pups. While ashore they are unable to forage. It was once thought that most true seals fasted for the entire lactation period (4–45 d, depending on the species), since this process had been demonstrated in large species such as grey seals (*Halichoerus grypus*; approximately 200 kg) and northern elephant seals (*Mirounga angustirostris*; approximately 500 kg). It is now clear that most if not all the smaller species (less than 100 kg) feed during the latter part of lactation, apparently because maternal reserves are insufficient to cover the entire lactation period (Oftedal *et al.* 1987a; Bowen *et al.* 1992; Boness *et al.* 1994; Boness & Bowen, 1996).

All phocids that have been studied produce milks that in mid to late lactation are very high in fat (about 470–610 g/kg), low in sugar (≤ 15 g/kg) and have a very low percentage of energy provided by protein (≤ 10 ; Oftedal *et al.* 1987a, 1988; Boness & Bowen, 1996). This composition is consistent with that expected of fasting mammals. In some species early-lactation milk is lower in fat and has a higher proportion of energy provided by protein, apparently to support the needs of young pups for gain in lean M.

Phocid pups generally gain M rapidly during lactation, but a surprising proportion of this gain is fat in subcutaneous blubber. At the extreme, about three-quarters of the gain in M of the sucking hooded seal (*Cystophora cristata*) pup is blubber, and much of the remainder is visceral fat (Bowen *et al.* 1987; Oftedal *et al.* 1989, 1993b). In this species most of the gain in lean M occurs before birth, and the postnatal period is devoted to fat accumulation. The pup contains 140 g fat/kg at birth and 450 g fat/kg at 4 d of age when weaned (Oftedal *et al.* 1993b). The high fat content of weaned phocid pups (330–480 g/kg) is essential for survival of the postweaning fast that lasts for 1.5–10 weeks (Muelbert & Bowen, 1993).

The low protein level in phocid milk reflects the small proportion of pup gain that is lean M. In the hooded seal only 5 % of the energy in the milk is protein, the lowest protein level of any mammalian milk (Oftedal *et al.* 1988).

The rate of milk energy output varies inversely with the duration of lactation among phocids (Oftedal *et al.* 1996). This relationship is perhaps not surprising because (1) all phocids rear only one pup, (2) M of the pup at weaning is a similar percentage of the maternal M (23–34 %) in all species (Bowen, 1991), and (3) pups in all species

accumulate large amounts of body fat (Muelbert & Bowen, 1993). Thus, the lactating female must transfer sufficient milk nutrients and energy to allow the pup to achieve target lean mass and fat mass by the time of weaning, even though the time allotted for lactation varies from 4 d in the hooded seal to about 45 d in the Weddell seal (*Leptonychotes weddellii*). The milk energy output rates are 4–5 and 0.8 MJ/kg M^{0.75} per d in hooded and Weddell seals respectively (Tedman & Green, 1987; Oftedal *et al.* 1993b; Lydersen *et al.* 1997). In contrast, the highest milk energy outputs in terrestrial non-fasting mammals are about 1 MJ/kg M^{0.75} per d, in species suckling large litters (Oftedal, 1984). Phocids sustain remarkably high rates of milk energy output, even though they fast for much of or throughout lactation.

The proportions of maternal body fat and protein exported in milk can be estimated in three species of large phocids that fast throughout lactation, i.e. hooded seals (179 kg), grey seals (207 kg), and northern elephant seals (509 kg). The total milk outputs (kg) in these species have been measured as 30–31, 48 and 138 (Iverson *et al.* 1993; Oftedal *et al.* 1993b; Lydersen *et al.* 1995, 1997), representing about 17, 23 and 27 % maternal M respectively. The corresponding fat outputs are 18, 27 and 59 kg, while protein outputs are 1.6, 4.7 and 10.6 kg.

At parturition, lipids account for 30–50 % maternal M in phocids (Costa *et al.* 1986; Reilly & Fedak, 1990; Ryg *et al.* 1990; Costa, 1991; Bowen *et al.* 1992; Beck *et al.* 1993). If an initial fat content of 400 g/kg M is assumed, milk lipid outputs of the hooded, grey and northern elephant seals represent mobilization of 25, 33 and 29 of the maternal body fat respectively. Milk secretion also entails transfer of 7, 17 and 16 % of the maternal body protein, and 23, 30 and 26 % of the maternal body energy into milk in these three species respectively. The low protein transfer of hooded seals is consistent with the fact that pups show little if any gain in lean M during lactation. The similar values for grey and northern seals are probably more typical of phocids that fast throughout lactation.

Data are also available on milk production by species which are known or thought to feed during lactation, such as harp seals (*Phoca groenlandica*), harbour seals (*Phoca vitulina*), ringed seals (*Phoca hispida*), bearded seals (*Erignathus barbatus*) and Weddell seals (Tedman & Green, 1987; Bowen *et al.* 1992, Lydersen & Hammill, 1993; Lydersen & Kovacs, 1996; Lydersen *et al.* 1996; Oftedal *et al.* 1996), but the proportion of milk nutrients derived from maternal reserves *v.* dietary intake is difficult to determine. For example, it is likely that a portion of the 77 kg fat and 13 kg protein secreted in milk by Weddell seals (Tedman & Green, 1987) is of immediate dietary origin; otherwise 43 % of the maternal body fat and 22 % of the maternal body protein would be required as substrates for milk synthesis. Bowen *et al.* (1992) reported that harbour seals depleted maternal fat reserves in the first four-fifths of lactation, and argued that this species was obligated to feed because fat reserves were inadequate to support both maintenance and lactation costs for more than 2 weeks. A subsequent study revealed that most harbour seals did in fact begin to feed by 12 d postpartum (Boness *et al.* 1994).

The baleen whales (Cetacea: Mysticeti)

The baleen whales include three families: the great baleen whales or rorquals (Balaenopteridae), the right whales (Balaenidae) and the grey whale (Eschrichtidae). Species in all three families undergo long migrations from summer feeding grounds to winter breeding grounds, where calves are born and nursed while mothers fast during part of or throughout lactation (Oftedal, 1997). Data on mammary anatomy, body composition and milk composition obtained from whaling ships and whaling stations can be used to estimate reproductive costs of some species (Lockyer, 1984; Oftedal, 1997).

The great baleen whales have a phenomenal ability to acquire and deposit excess nutrients in blubber and other tissues during relatively brief foraging periods in highly productive polar and cold temperate waters. Based on morphometric data, Lockyer (1984) estimated that pregnant blue whales (*Balaenoptera musculus*; estimated M 119 000 kg) deposited 45 000 kg as blubber during the summer foraging season, and that fin whales (*Balaenoptera physalus*; 65 000 kg) deposited 16 000 kg during the same period. These whales then migrate to tropical or warm-temperate waters to give birth and nurse their young before their return to the foraging grounds the following summer. It is believed that the lactating females fast, or eat very small amounts, during the 5–7-month lactation period (Oftedal, 1997). Yet the calves grow rapidly. Blue whale calves, for example, gain about 17 000 kg during the sucking period (Lockyer, 1981).

During mid to late lactation the great baleen whales produce milks containing (g/kg) 300–400 fat, 110–150 protein, and probably 10–20 sugar (Oftedal, 1997). Most of the energy transferred to calves is as lipids, restricting the need for maternal gluconeogenesis. The amounts of milk transferred have not been measured, but can be predicted based on mammary gland mass and calf growth rates. On the assumptions that cetacean mammary glands produce 0.5–1.3 kg milk/kg mammary mass, and that cetacean calves require 2–4 kg milk/kg M gain, blue whales are predicted to produce about 220 kg milk/d (range of estimates 110–320 kg/d; Oftedal, 1997). As blue whale milk contains 18 MJ/kg, this is equivalent to an energy output of 0.72 MJ/kg M^{0.75} per d, similar to estimates for Weddell seals and to peak outputs for terrestrial mammals with large litters.

The rate of milk energy output may appear normal for a mammal, but the immensity of the blue whale and the fact that lactation persists for 6 months result in staggering predictions of the amounts of milk (about 40 000 kg), fat (about 16 000 kg), protein (4 500 kg) and energy (about 710 000 MJ) transferred to the calf. Assuming a postpartum M of 120 000 kg, and a body fat content of 400 g/kg, the predicted amounts of fat, protein and gross energy mobilized are equivalent to about 33, 28 and 32 % of the initial body contents of these constituents respectively. While these levels of fat and energy mobilization are consistent with data for other fasting mammals, it is improbable that a mammal could lose more than one-quarter of body protein and not suffer adverse consequences. Perhaps blue whales feed during the return migrations to

their summer foraging grounds before calves are weaned, as has been reported for other species (Lockyer, 1984; Swartz, 1986).

The remarkable ability of great baleen whales to store lipids was their undoing, as it made their harvest for whale oil lucrative, despite the enormous costs of equipping and running floating factories in remote polar seas (Tønnessen & Johnsen, 1982).

Summary

A number of mammals appear to have taken advantage of the nutrient storage capabilities associated with large size and the reduced mammary glucose demand associated with production of high-fat low-sugar milks. In these species, females fast for part of or throughout lactation, and maternal reserves are heavily exploited for milk production. For example, lactating females appear to transfer one-fifth to one-third of body lipids into milk lipids during parts of or throughout lactation in fur seals, bears, true seals and great baleen whales (Fig. 1). The relative amount of the gross energy of the body transferred into the milk is similar, about one-sixth to one-third (Fig. 1).

Mobilization of body protein appears to vary to a greater degree among taxa (Fig. 1), largely due to differences in milk protein content. Some species can afford to produce relatively low-protein milks, either because of slow growth rates of the young (e.g. fur seals and bears) or because the proportion of postnatal growth that is lean mass is small (e.g. true seals). Nonetheless, protein transfers via milk are equivalent to 16–18% of the maternal body protein in some species of fasting seals and bears. The prediction of even higher protein transfer in baleen whales seems improbable and suggests that females feed in late lactation.

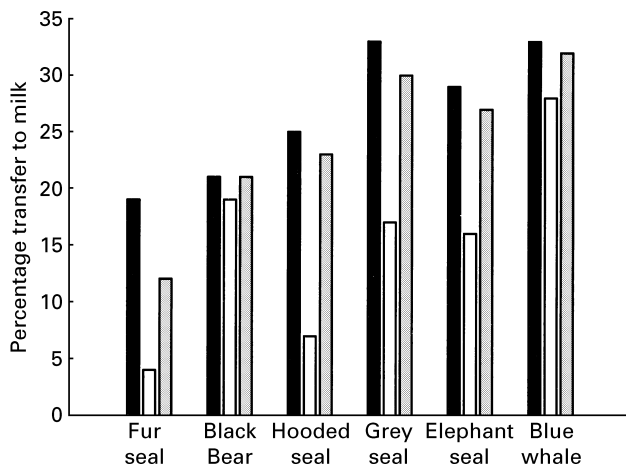


Fig. 1. Estimates of the percentages of maternal body constituents (■, fat; □, protein; ▨, energy) transferred into milk in species that fast during part of or all lactation. Values for all species except the blue whale (*Balaenoptera musculus*) are based on isotope measurements of milk production (for references, see pp. 101–103); the blue whale values are predictions based on mammary gland mass and calf growth (see p. 103). The species are as follows: Antarctic fur seal (*Arctocephalus gazella*), black bear (*Ursus americanus*), hooded seal (*Cystophora cristata*), grey seal (*Halichoerus grypus*), northern elephant seal (*Mirounga angustirostris*) and blue whale.

The fact that some large mammals have so successfully exploited an ability to store nutrients and mobilize them during lactation suggests that this strategy may be more important in other mammals than is generally recognized.

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