Energetics

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I. Introduction

Energetics provide a method to quantitatively assess the effort animals spend acquiring resources, as well as the relative way in which they allocate those resources. Energy flow models are analogous to cost–benefit models used in economics. Costs take the form of energy expended to acquire and process prey, and to maintain body functions. The energetic benefits are manifest as food energy used for growth and reproduction. Measurement of energy acquisition and allocation provide a quantitative assessment of how animals organize their daily or seasonal activities, and how they prioritize their behaviors. Thus, energy flow can be described as what goes into the animal as food and what comes out in the form of growth, reproduction, repair, waste, or metabolic work. Survival requires a positive balance between the costs of maintenance and the acquisition of food energy. If a marine mammal cannot compensate for decreases in energy acquisition, it must either reduce its overall rate of energy expenditure or utilize stored energy reserves. Conversely, in order to grow and reproduce, animals must obtain more energy than is needed to survive. Marine mammals undergo profound variations in this least or famine dynamic equilibrium as they can gain significant amounts of food energy while feeding in highly productive environments, followed by prolonged negative energy balance while fasting during migration or reproduction (Brodie, 1975; Costa, 1993; Lockyer, 1993) (Fig. 1).

The balance of how energy acquisition and expenditure is achieved differs for individual species and environments. For
some species, sea otters (*Enhydra lutris*), sea lions, and fur seals (*Otaridae*), very high rates of energy expenditure are met by high rates of energy acquisition (Costa and Williams, 2000). These animals preferentially live in nearshore environments or upwelling regions where food is abundant (Costa, 1993). Sirenians represent the opposite extreme. These marine mammals exhibit comparatively low existence costs and are able to survive on a low-quality diet. They have adapted to a diet of grasses that is in high abundance but of low quality, energetically. They are able to do this because; they live in the climatically benign tropics where maintenance costs are low (Gallivan and Best, 1980; Gallivan et al., 1983; Irvine, 1983).

The seasonal migrations of large cetaceans demonstrate this interrelationship between energetic demand, energy availability, and local productivity (Brodie, 1975). Although maintenance costs may be elevated in polar regions, the ability to take advantage of the seasonally high productivity associated with the sea ice during the polar summer more than compensates (Fig. 2). When confronted with the high energetic costs of reproduction and of winter conditions, the mysticete whales opt for the more benign tropics. Further, their large body size makes the cost of migration extremely low (see Locomotion, this volume). While prey availability may be low in the tropics, so too are the existence costs, especially for a large animal that is able to utilize energy reserves stored in the blubber.

A conceptual diagram of the relationship between energy acquisition and allocation is shown in Fig. 1. The rate of energy consumed by the animal is referred to as Ingested Energy (IE). The energy that remains after the losses associated with the production of feces and urine is the Metabolic Energy (ME). This is the energy available for maintenance and repair, growth or reproduction. Energy expended for maintenance includes key processes such as basal metabolism, digestion (heat increment of feeding, HIF), thermoregulation, and activity (locomotion, grooming, feeding, etc.). The rate of prey energy acquired is directly related to the availability and quality of prey. As prey becomes less available, the cost of finding it increases and the animal spends a greater proportion of its time and therefore energy searching for it. Eventually, there is a threshold when more energy is spent searching for prey than is obtained and the animal goes into negative energy balance (Winship et al., 2002; Rosen and Trites, 2005). While the best situation is to have access to abundant high energy prey, in some scenarios low-quality prey that is more abundant may be more optimal than searching for high-quality prey that is difficult to find.

### II. Energy Acquisition

Not all of the ingested material consumed is digestible. Food energy remaining after digestion and elimination of Fecal Energy (FE) is known as the Apparently Digested Energy (ADE). The proportion of ADE to IE is called the assimilation efficiency and ranges from 88% to 97.9%, for a diet of fish to 72.2% for invertebrate prey with a high chitin content (Martensson et al., 1994; Lawson et al., 1997; Costa and Williams, 2000; Rosen and Trites, 2000). The assimilation efficiency decreases as the rate of prey intake increases, but is greater when a diet composed of different species of fish with
different proximate compositions is consumed (Trumble and Castellini, 2005). Sirensians extract less energy from their food than other marine mammals (84.6%), because plant material, which contains cellulose and requires bacterial fermentation to digest, is harder to digest. However, they are more efficient than other hindgut fermenters, such as horses, Equus caballus (45–59%) (Burn, 1986).

Chemical energy lost as urea and other metabolic end products in the urine is defined as Urinary Energy (UE). Metabolizable Energy (ME) is the net energy remaining after fecal and urinary energy loss, and represents the energy available for growth or reproduction and for supporting metabolic processes such as work (locomotion) and respiration (thermoregulation, maintenance metabolism, HIF). The ME for pinnipeds varies between 78.3% for a squid diet to 91.6% for an anchovy diet (Costa and Williams, 2000).

III. Energy Expenditure
A. Cost of Maintenance Functions

Maintenance costs are those associated with homeostasis and include basal metabolism, HIF, repair (molt, fighting disease, and/or parasites), thermoregulation, and activity (see Thermoregulation and Locomotion, this volume).

1. Basal Metabolism It has generally been assumed that the basal metabolic rates of aquatic mammals are elevated when compared to terrestrial mammals of similar size. The current view of basal metabolic rates of marine mammal is more complex as many studies did not conform to standardized criteria for measurements of basal metabolism (Lavigne et al., 1986). These criteria require that the subjects be adults, resting, thermoneutral, non-reproductive, and post-absorptive. This has been further confused by the expectation that all marine mammals should employ the same metabolic response. Specialization for marine living has occurred independently in three mammalian orders: the sirenians, cetaceans, and carnivores. Further, within the carnivores there are three separate transitions to a marine existence: the sirenians, cetaceans, and carnivores. Further, within the carnivores there are three separate transitions to a marine existence: pinnipeds, sea otters, and polar bears, Ursus maritimus. Based on this diversity, we might expect different metabolic adaptations between the groups (Fig. 3). West Indian manatees, Trichechus manatus, have BMRs lower than values predicted, while phocid seals have BMRs closer to those of similar sized terrestrial mammals. Conversely, sea otters, otariids, and odontocetes appear to have BMRs greater than terrestrial mammals of equal size.

The BMR of an animal is not constant, but varies seasonally (Rosen and Renouf, 1995; Williams et al., 2007), with the animal’s nutritional state (Rosen and Trites, 1999), as well as with the animal’s body composition (Rea and Costa, 1992). Some species such as sirensians and walrus, Odobenus rosmarus, have dense bone, whereas seals may be composed of as much as 50% fat. When metabolic rates are expressed relative to body mass, a disproportionate amount of fat or particularly dense bone will lower the apparent metabolic rate. This is due to the low metabolic rates of bone and adipose tissue in comparison to lean tissue. Many marine mammals undergo prolonged fasts that are accompanied by profound changes in body composition. Most of the mass change during fasting is due to loss of adipose tissue with a comparatively smaller change in lean tissue. For example, northern elephant seal females, Mirounga angustirostris, lose 42% of their initial mass, but of this only 14.9% comes from lean tissue with 57.9% coming from adipose tissue (Costa et al., 1986). This results in an overall change in body composition of 39% fat at parturition to 24% fat at weaning (see Pinnipedia Physiology, this volume). Since lean mass is the primary contributor to whole animal metabolism, the animals whole body metabolism is likely to change little even though there has been a major change in its body mass (Rea and Costa, 1992).

The ability to digest and process the greater amount of prey associated with the higher metabolic rates of marine mammals may have also required changes in their morphology. Specifically, all carnivorous marine mammals, regardless of their ancestry (carnivore or herbivore) have comparatively longer small intestines than similarly sized terrestrial carnivores. Further, there is a high correlation between small intestine length and BMR in mammals (Williams et al., 2001).

2. Heat Increment of Feeding When food is consumed, the animal’s metabolic rate increases over fasting levels. The HIF, also known as the Specific Dynamic Action (SDA), may be considered the “tax” that is required to process food energy for conversion to Metabolizable Energy (ME). The magnitude of energy allocated to HIF varies between 5% and 17% of the ME (Costa and Kooyman, 1984; Markussen et al., 1994; Rosen and Trites, 1997). In addition, the duration of HIF following a meal will depend on the amount of food consumed and its composition. In many mammals, the HIF is considered excess or waste heat. However, sea otters incorporate the additional heat produced from HIF to meet their high thermoregulatory costs associated with their small size (they are the smallest marine mammal) (Costa and Kooyman, 1984). While grooming, feeding, and swimming sea otters use the heat produced from activity to supplement their thermoregulatory needs, while at rest sea otters incorporate the heat produced from HIF to augment their thermoregulatory needs (Fig. 4).

3. Fur vs Blubber It is important to consider the potential differences in the energy budgets of animals that use fur or blubber for insulation. The overall time-energy budget of an animal that uses fur (fur seal or sea otter) is fundamentally different from an animal that uses blubber (sea lion, seal, or dolphin). Although fur is not a living...
Figure 4  The thermal budget of sea otters relies on heat production above BMR (or SMR). The contribution of HIF (or SDA) to the overall metabolism is highest immediately after feeding and reaches zero within 390 min after feeding. As HIF decreases the animal becomes more active and thus compensates for the decrease in heat production from HIF (Costa and Kooyman, 1984).

tissue, it requires the maintenance of an air layer, which is done by frequent grooming. Sea otters spend up to 16% of their day grooming. While sea lions, seals and dolphins, spend no time grooming, they must take in sufficient food to lay down a thick blubber layer, which is a living tissue and must be supplied with blood. Furthermore, blubber serves dual roles as an insulator and as an energy store. During fasting or periods of low food availability a marine mammal must balance its utilization of blubber for energy needs with the potential loss of the blubber layer as an insulator. For pinnipeds a way of increasing blood flow to the skin and keeping thermoregulatory costs low while ashore is to huddle together. This reduces their effective surface area that is exposed to the cold (Fig. 5). Such behavior is commonly observed in cold climates and can change during the day. For example, in the morning when it is cold, animals clump together and as it gets warmer they separate. Finally, huddling behavior is less common in fur seals, as there isn't much of an incentive to huddle if you use fur for insulation.

B. Cost of Growth and Reproduction

For growth and reproduction to occur, an animal must acquire energy and nutrients in excess of that required for supporting maintenance functions. These additional energetic costs vary with the species of marine mammal, the sex, and reproductive pattern. In pinnipeds, polar bears, sea otters (and probably mysticetes and sireni ans) the cost of reproduction in males is limited to the cost of finding and maintaining access to estrous females. Evolution favors a pattern of energy expenditure that maximizes reproductive success in males. The costs associated with reproduction in aquatic and terrestrially breeding males is quite similar when normalized for differences in body mass. Larger body size is preferred in terrestrially breeding male pinnipeds since it confers both an advantage in fighting and allows the male to maintain terrestrial territories longer (Fig. 6) (see Pinnipedia Physiology, this volume). In addition, larger animals can fast longer because they have a lower mass specific metabolic rate than smaller animals (Costa, 1993). In species that compete for females in the water, males are comparatively smaller than the species that breed on land. For the aquatic breeders, underwater agility is more important than large size when competing for mates.

The cost of reproduction for females can be broken down into the energetic requirements of gestation and lactation. The cost of gestation is small relative to the cost of lactation. Even given the strikingly different reproductive patterns in marine mammals, there is little variation in fetal mass at birth among marine mammals, but as a group they appear to invest more energy into fetal birth mass (and thus more into gestation) than terrestrial mammals (Fig. 7). This higher investment in gestation by all marine mammals except polar bears is associated with the production of precocial young (Fig. 8). The young of cetaceans, sireni ans, pinnipeds, and sea otters need to be capable of dealing with life in the water or on a crowded rookery within seconds of birth. As a group marine mammals exhibit considerable variation in both the duration and pattern of maternal investment (Fig. 9). Phocid seals and mysticete whales have extremely short lactation durations, which are compensated for by higher rates of energy transfer that enable the young to grow rapidly (Fig. 10).

Although phocid pups are weaned early, they still rely on maternally derived energy, stored as blubber, for weeks or months after weaning. The disadvantage of this rapid growth is that most of the
mass and energy is stored as fat with proportionately little protein. The advantage of longer lactation is that young get more protein and other nutrients allowing greater growth of lean tissue. However, longer lactation is energetically more expensive (Costa, 1991a, b, 1993).

1. Variation in Milk Composition The rapid growth of marine mammal young is made possible by the ingestion of extremely lipid rich milk. With a few exceptions, terrestrial animals produce milk that is low in fat; cows, Bos taurus and humans, Homo sapiens, produce milk that contains 3.7% and 3.8% milk fat, respectively. Lipid-rich milk allows the mother to transfer high levels of energy in a very short period. Hooded seals, Cystophora cristata, are most impressive with a 4-day lactation interval and a milk fat of 65% lipid (Bowen et al., 1985). In view of this, it is not surprising that marine mammals with the highest growth rates produce milk with the highest lipid content.

Lactation also enables mothers to optimize the delivery of energy to their young. The energy content of the milk is independent of the type or quality of prey consumed, or the distance or time taken to obtain it. Although milk is ultimately derived from the prey consumed, a mother can process, concentrate, or utilize stored reserves to produce milk. For example, some species feed on fish, while others feed on fish or squid. Yet, all of these species provision their offspring with milk of significantly greater energy density than the prey consumed (Costa, 1991b).

2. Body Size and Maternal Resources: The Role of Maternal Overhead Fasting during lactation is a unique component of the

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**Figure 7** Birth mass plotted in relation to maternal mass for marine and terrestrial mammals. Species of marine mammals included are: Odontoceti—Inia geoffrensis, Pontoporia blainvillei, Stenella attenuata, Globicephala melaena, Physeter macrocephalus, T. truncatus, Phocoena spinipinnis, P. phocoena, Delphinapterus leucas; Mysticeti—Balaenoptera musculus, B. physalus, B. acutirostrata, B. borealis, Megaptera novaengliae, Eschrichtus robustus; Phocidae—Mirounga angustirostris, M. leonina, Cystophora cristata, Phoca vitulina, P. hispida, Leptonychotes weddelli, Monachus schauinslandi, Pagophilus groenlandicus, Erignathus barbatus, Lobodon carcinophagus, Histriophoca fasciata, Halichoerus grypus; Otariidae—Arctocephalus gazella, A. forsteri, A. galagagoensis, A. tropicalis, A. pusillus, Callorhinus ursinus, Zalophus californianus, Neophoca cinerea, Enunatopias jubatus, Otaria byronia; Sirenia—Dugong dugon, Trichechus manatus.

**Figure 8** A harbor seal (Phoca vitulina), mother and pup on a California beach. The pup was recently born and shows the extreme level of precociality typical for marine mammals. In harbor seals the pup is born with the adult pelage and it can go to sea within an hour of birth. Photograph by Dan Costa.

**Figure 9** Time to weaning plotted as a function of maternal mass for marine mammals. Lactation durations of phocid seals and mysticete whales are shorter than in all other marine mammals. Species are same as in Fig. 3.

**Figure 10** Growth rate of suckling marine mammals as a function of maternal mass. Lines represent least squares regressions for each taxonomic group. Species are same as in Fig. 3.
life history pattern of marine mammals (Costa, 1993; Oftedal, 2000). With the exception of bears, no other mammal is capable of producing milk without feeding. By undertaking this energetic challenge, mysticetes and pinnipeds are able to separate where and when they feed from where and when they breed. In mysticete whales, this allows them to feed in the highly productive polar regions of the world’s oceans, but retain the thermal advantage of breeding in the calm tropical regions (Fig. 2) (Brodie, 1975). Migrating to warmer waters for parturition reduces the thermal demands on the newborn calf and additional thermal savings for the mother.

Among pinnipeds, the separation of feeding from lactation is necessary to allow for terrestrial parturition (Bartholomew, 1970). Most phocids store sufficient energy reserves for the entire lactation period, whereas all otariids must feed during lactation (see Pinnipedia Physiology and Pinniped Reproduction, this volume) (Costa, 1991a, b). A phocid mother typically remains on or near the rookery continuously from the birth of the pup until it is weaned; whereas milk is produced from body reserves stored prior to parturition (Fig. 11). Although some phocids feed during lactation, most of the maternal investment is derived from body stores. Their reproductive pattern is less constrained by the time it takes to travel and exploit distant prey, which allows utilization of a more dispersed or patchy food resource (Costa, 1993). By spreading out the acquisition of prey energy required for lactation over many months at sea, northern elephant seal females only need to increase their daily food intake by 12% to cover the entire cost of lactation.

The ability of a marine mammal female to fast while providing milk to her offspring is related to the size of her energy and nutrient reserves and the rate at which she utilizes them. When food resources are far from the breeding grounds, as may occur for some phocids and large mysticete whales, the optimal solution is to maximize the amount of energy and nutrients provided to the young and to minimize the amount of energy expended on the mother. The term “metabolic overhead” refers to the amount of energy a female expends on herself while onshore (seals) or while in the calving grounds (whales). Larger females have a lower metabolic overhead than smaller females. This is because maintenance metabolism scales as mass$^{0.75}$, and fat stores scale as mass$^{1.0}$. As body size increases, energy reserves increase proportionately faster than maintenance metabolism.

3. Energy Investment and Trip Duration  Many phocids fast throughout the lactation interval, whereas otariid females feed intermittently between suckling bouts onshore (Fig. 12) (Costa, 1991a, b). Otariid mothers modify the timing and patterning of energy and nutrient investment to optimize energy delivery to their young (Boyd, 1998; Trillmich and Weissing, 2006). Otariid mothers making short feeding trips that provide their pups with less milk energy than mothers that make long trips. In comparison to otariids, phocids may have a reproductive pattern that is better suited for dealing

**Figure 11**  A recently born northern elephant seal (Mirounga angustirostris) pup suckles from its’ mother (below) is compared to a recently weaned pup (30 days old). The mother does not eat or drink during the 26- to 28-day lactation interval, and after weaning the pup fasts for 2–3 months before going to sea. Elephant seals, like many true seals, fast during the entire lactation interval. Photograph by Dan Costa.

**Figure 12**  A Galapagos sea lion (Zalophus wollebaeki) female suckling her pup on left, and on a trip to sea on right. Fur seals and sea lions intermittently suckle their pup on shore between trips to sea to forage. Photograph by Dan Costa.
with dispersed or unpredictable prey, or prey that is located at great distances from the rookery (Costa, 1993). However, fasting during lactation places a limit on the duration of investment and this limits the total amount of energy that a phocid mother can invest in her pup.

Phocids are buffered from short-term fluctuations in prey availability due to their unique reproductive pattern. In phocids, reproductive performance (maternal investment) during a given season reflects prey availability over the preceding year and represents the mother’s foraging activities over a much larger spatial and temporal scale than the foraging activities of otariids (Costa, 1993). It follows that the weaning mass of a phocid pup is an indicator of the mother’s foraging success over the previous year, whereas the subsequent post-weaning survival of the pup is related to both its weaning mass (energy reserves provided by the mother) and the resources available to the pup after weaning.

C. Field Metabolic Rates

A number of approaches have been used to study the metabolic rate of animals at sea. One approach, time budget analysis, sums the daily metabolic costs associated with various activities (Williams et al., 2004). Other methods rely on predictive relationships between physiological variables and metabolic rate. For example, metabolic costs can be indirectly assessed by measurements of changes in body mass and composition, variations in heart rate or ventilation rate, or with the dilution of isotopically labeled water (Folkow and Blix, 1992; Boyd et al., 1999; Costa and Gales, 2000).

Field metabolic rates (FMR) provide insight into the energetic strategies used by marine mammals (Costa, 1993; Costa and Gales, 2003). The best data exist for pinnipeds and the common bottlenose dolphin, Tursiops truncatus (Fig. 13), and indicate that foraging otariids and bottlenose dolphins expend energy at 6 times the predicted basal metabolic level (Costa and Williams, 2000). In contrast, the metabolic rate of diving elephant seals (Mirounga spp.) and Weddell, Leptonychotes weddellii, seals are only 1.5–3 times the predicted basal rate (Castellini et al., 1992). The lower diving metabolic rate of phocid seals contributes to their superb diving ability (Costa, 1993) (see Diving Physiology, this volume). The importance of the thermal environment on field metabolic rate can also be seen in Galapagos fur seals, Arctocephalus galapagoensis, which due to the warm equatorial climate have a substantially reduced field metabolic rate compared to other otariids (Trillmich and Kooyman, 2001). An interesting consequence of the high metabolic rate of marine mammals is that the presence of a few foraging individual can have a significant impact on community structure (Estes et al., 1998; Springer et al., 2003).

FMR are quite variable both between and within species (Fig. 13). Such variation is thought to be associated with year-to-year changes in both the abundance and availability of prey (Costa, 2007). In response to reduced availability of prey, fur seals and sea lions mothers increased their foraging effort in an effort to keep the duration of their foraging trip the same. However, there reaches a point where they can no longer increase their foraging effort and have to spend more time at sea to obtain the same amount of prey energy. If a mother spends more time to deliver the same amount of energy, the offspring receives less overall energy. As a result, more of the offspring’s energy is spent on maintenance and its growth will slow and in the worst case the pup will eventually die.

1. Energetics of Prey Choice

The amount of work, and therefore energy expenditure that an animal puts into locating prey varies as a function of the energy content, availability, and location of the prey both geographically as well as its depth in the water column. Both size and proximate composition (fat, carbohydrate, protein, and water content) affect the energy content of prey. Prey availability varies as a function of the absolute abundance of prey (amount of prey per unit of habitat) and its distribution in the environment. A predator is more efficient when foraging on prey that is clumped than on prey that is evenly dispersed. Similarly, prey that is near the surface is easier to obtain than prey located at depth. Marine mammals forage in areas where prey has been concentrated as a result of oceanographic processes like eddies, fronts, and upwelling regions associated with bottom topography.

Sea otters provide an excellent example of the factors that determine the energetics of prey choice (Fig. 14) (Riedman and Estes, 1990). In recently occupied areas, sea otters feed on preferred prey items like clams, abalone, Haliotis spp., or sea urchins. In such environments they find large, energy-rich, abundant prey that is easy to handle, consume, and digest. In such situations, lower quality prey items (turban snails, sea stars, mussels, chitons) are generally not eaten. These items may be abundant, but they are energy poor, and difficult to eat and digest. As the abundance and size of their preferred prey declines, sea otters switch to less preferred but more accessible prey like turban snails, kelp crabs, and in some cases, chitons and sea stars. Some sea otters specialize on different types of prey and are more efficient predators than non-specialists (Estes et al., 2003).
Polar bears represent another example of optimal prey choice and its relation to the prey energy quality. Feeding predominately on ring seals, *Phoca hispida*, polar bears eat the energy-rich blubber layer and leave behind the lean “core” of the carcass (Stirling and McEwan, 1975). Due to its high lipid content the blubber has a per unit mass energy content almost 10 times greater than that of the lean tissue of the ring seal. Thus, polar bears consume the most energy dense part of the ring seal and then move on to find another kill.

2. Variations in Foraging Energetics Different foraging behaviors are associated with different metabolic costs. For example, in sea lions benthic foraging is more expensive than epipelagic or near surface feeding (Costa and Gales, 2000, 2003). The gulping behavior of blue, *Balaenoptera musculus*, fin, *B. physalus*, and other whales of the family Balaenopteridae also appears to be quite costly due to the tremendous drag created as they open their enormous mouths to engulf entire schools of prey (Croll et al., 2001). The blue whale finds a school of krill, and opens its mouth engulfing the entire school of krill. The whale then expels the water through its baleen plates, retaining the krill in its mouth. Consider how much drag, and thus increased effort, it takes to leave behind the lean “core” of the carcass (Stirling and McEwan, 2001–2002). Thus, polar bears consume the most energy dense part of the ring seal and then move on to find another kill.

*See Also the Following Articles*

Diving Physiology ▪ Pinniped Physiology ▪ Thermoregulation

References


