Metabolic Rates of Endotherms & Ectotherms

Metabolism is the rate at which energy is used by an organism. An individual's metabolic rate (MR) is affected by a number of factors, such as activity level, digestion, stress, illness and pregnancy. Thus, to compare different individuals, or even different species, we need a standard. In endotherms, the minimum metabolic rate is called the Basal Metabolic Rate (BMR). BMR is measured when the subject is quiet but awake. It is the minimum amount of energy required to remain alive and functional (non-functional states, such as sleeping, hibernation and coma, can cause MR to go below the Basal level). In ectotherms, the resting MR at a given temperature is the Standard Metabolic Rate (SMR).

Two of the main determinants of BMR are Temperature and Body Mass. For comparing humans, we assume that body temperature is the same for everyone, so the major determinant is body mass. Human physiologists often include other, minor determinants of BMR: Gender (males have a higher BMR than females, even after taking into account the difference in mass), Age (BMR decreases with increasing age), and Thyroid hormone level (thyroid hormones can stimulate metabolism).

Temperature.

Some animals have very high rates of metabolic heat production. Such animals are called endotherms, because their major source of heat is internal, in contrast to ectotherms, which generally rely on environmental sources of heat. However, the difference between homeotherms and heterotherms is based on the stability of body temperature (Figure 1). Homeotherms maintain a constant body temperature, whereas the body temperature of heterotherm can change (often, it is the same as the environmental temperature).

Although most homeotherms are endotherms (the reliability of an internal heat source is practically required to maintain a constant body temperature), it is possible for some homeotherms to be ectothermic. For example, certain desert insects maintain a relatively constant body temperature by moving between sunlight and shade (but only during daytime), and the body temperature of large ectotherms (*e.g.*, crocodiles over 500 kg) changes very slowly due to thermal inertia.

Similarly, most heterotherms are ectotherms, but some heterotherms can be endothermic. For example, some heterotherms (*e.g.*, large flying insects) generate significant amounts of heat when they are active, and naked mole rats and some desert rodents allow their body temperature to change more than other mammals. Furthermore, some animals can adopt different thermoregulatory strategies depending on the situation; for example, mammals that hibernate allow their body temperature to fall and even to fluctuate with the surrounding temperature.

Why are some species ectotherms while others are endotherms? There are trade-offs; an advantage to one type of animal is a disadvantage to the other type. Endotherms are constantly generating large amounts of heat, which requires large amounts of food and oxygen, but then they have a reliable source of heat to maintain a high body temperature and high level of activity. Ectotherms do not expend any energy just for making heat, so they eat much less and use less oxygen, but then their body temperature and activity level are at the mercy of the environment (e.g., they may be sluggish in cool weather).

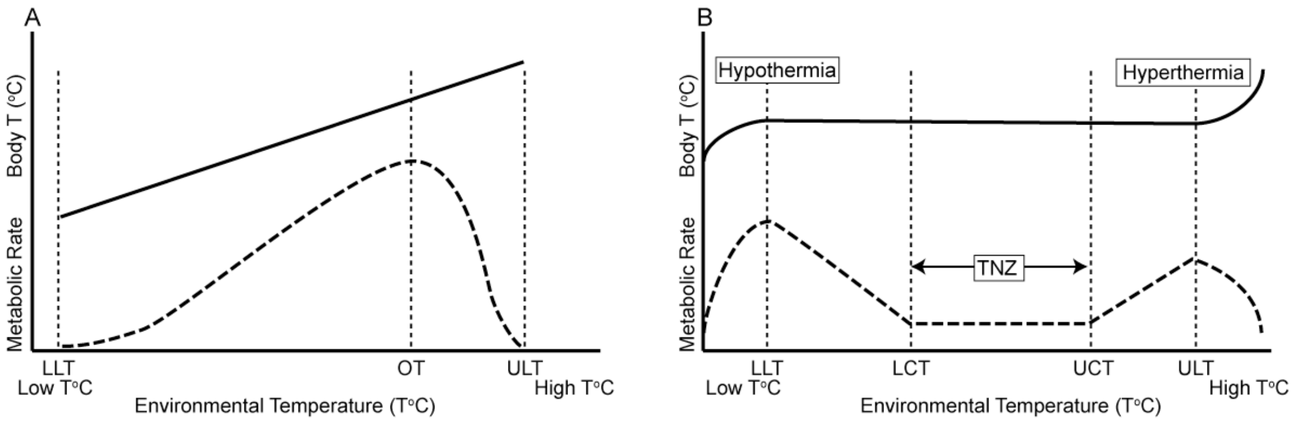

Figure 1. Relationship between body temperature, metabolic rate and environmental temperature. **A)** For heterothermic ectotherms, metabolic rate increases as temperature increases. **B)** In contrast, in homeothermic endotherms metabolic rate varies to maintain a relatively constant body temperature. In both graphs, solid line = body temperature; dashed line = metabolic rate; LLT = Lower Lethal Temperature; OT = Optimal Temperature; ULT = Upper Lethal Temperature; LCT = Lower Critical Temperature; UCT = Upper Critical Temperature; TNZ = thermal neutral zone.

Temperature and metabolic rate (MR) in heterotherms. Because biochemical reaction rates are temperature sensitive, the increased body temperature causes all biochemical reactions throughout the body to run faster. Some of these reactions are now making ATP faster, while others are using ATP faster, so energy usage is increased, and the overall MR increases. In other words, the change in body temperature causes the change in MR. This change in MR with temperature is described by the index Q_{10}. In general, a 10 °C increase in temperature will result in a 2-3 fold increase in MR.

$$Q_{10} = (MR_2 / MR_1)^{(10/(T2-T1))}$$

MR_1 was measured at temperature 1 (T1) and MR_2 was measured at temperature 2 (T2). We will use oxygen consumption (Vo_2) as an indicator of metabolic rate.

In a graph of metabolic rate versus environmental temperature for heterotherms, such as the cockroach, the metabolic rate increases as environmental temperature increases (Figure 1A). As environmental temperature increases, its body temperature increases. Note that this is a completely passive process, a result of heat transfer between the environment and the organism, just like the plastic models in the thermoregulation lab. Ectotherms can only control their body temperature behaviorally (*e.g.*, moving into warm sunlight or cool shade). The colony of Madagascar Hissing Cockroaches at the back of the lab has a heating pad underneath it. The cockroaches may warm-up by sitting by the heating pad, or they can move away to cool down. However, if the animal is trapped in one spot, then it has no more control of its body temperature than does a plastic model.

Temperature and metabolic rate (or Vo_2) in homeothermic endotherms. In a graph of MR versus environmental temperature for endotherms, such as humans, as environmental temperature increases, MR first decreases, then plateaus, then increases again (Figure 1B). The plateau region is called the thermal neutral (TNZ). TNZ is the range of environmental temperatures at which the organism does not use extra energy to maintain a constant body temperature, so these temperatures feel comfortable to the organism. The purpose of the increased MR, above the plateau level, is to maintain constant body temperature.

In the TNZ, heat can be lost to the environment through strictly passive heat transfer. Adjustments in heat transfer rate can be done without using any extra energy (*e.g.*, by constricting or dilating skin arterioles). But energy is still being used to generate heat in the TNZ, because endotherms are constantly generating heat throughout their bodies by their Basal metabolism. Since Basal metabolism is constantly generating heat, endotherms must constantly lose heat to the environment. At temperatures above or below this the thermal neutral zone, MR is increased above Basal metabolism. In other words, homeotherms actively change their MR to affect their body temperature.

At environmental temperatures below the TNZ, MR increases because energy is used to generate heat (e.g., by shivering). The colder the environmental temperature, more heat needs to be generated, so energy usage increases. At environmental temperatures above the TNZ, MR increases because energy is used to cool off (*e.g.*, by panting and sweating). At these higher temperatures, passive heat transfer is no longer sufficient, so now heat must be actively expelled, and these processes use energy. Since energy is being used, these processes themselves generate additional heat, which seems counterproductive. But as long as more heat is being expelled than is being generated, then the organism can maintain a constant body temperature despite the high environmental temperature.

2) Mass.

Basal metabolic rate (BMR) increases with increasing size. Why? Larger size means more cells are present, with each cell using energy, even at rest (*e.g.*, by ion pumps maintaining membrane potential). And the more cells that are present in the organism, the more total energy being used, even at rest, which means a higher BMR. If BMR values versus mass for species of different sizes are plotted on a log-log plot, the relationship is a straight line with a positive slope (Figure 2A). The equation that describes this relation is:

$$MR = a * Mass^b$$

where MR is metabolic rate (or oxygen consumption, VO_2) and b is the slope of the line. This is called an allometric equation, because it describes the relationship between a variable and body size (Figure 2A).

To compare different organisms of different sizes, we use relative-BMR (or mass-specific-BMR), which is equal to BMR divided by weight. Figure 2B shows that relative-BMR decreases with increasing mass. It seems counterintuitive, but larger animals consume *less* oxygen per gram of tissue than smaller animals. In other words, a gram of mouse muscle consumes more oxygen than a gram of elephant muscle.

The exact relationship between mass and BMR is complicated. First, not all cells use the same amount of energy. For example, muscles, neurons, and kidneys use a lot of energy, even at rest, while bone, connective, and adipose tissues use little energy. So, an individual with a high percentage of muscle mass would have a higher BMR than someone of the same weight but with a lower percentage of muscle. Similarly, males often have a higher percentage of muscle mass (due to the anabolic effects of testosterone) than females, so males tend to have a higher relative-BMR than females. Thus, differences in body composition can have minor affects on BMR, along with mass.

Anabolism refers to biochemical processes that consume energy during the synthesis of complex molecules (*e.g.*, DNA), while catabolism refers to processes that release energy during the degradation of complex molecules. Inefficiency in anabolic reactions, and all of the energy released during catabolism, are ultimately lost as heat. The rate at which energy is used can be

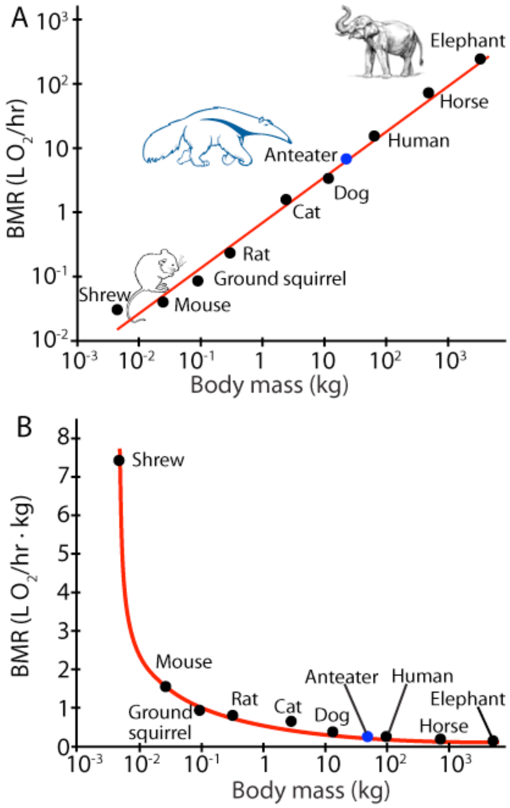

Figure 2. A) When Basal Metabolic Rate (BMR) is plotted against body mass on a log-log plot, the relationship is a straight line. B) A semi-log plot of relative-BMR versus body mass shows that small animals consume more O_2/kg than large animals.

measured either directly (as the rate of heat loss) or indirectly (as the rate of oxygen consumption, carbon dioxide production, or food consumption). Each of these methods has its own advantages and disadvantages. For oxygen consumption, it is technically easy to do, so this method is frequently used. For different types of food (carbohydrates, lipids, amino acids), the amount of energy released per oxygen molecule is different, but only slightly (the range is 4.5 - 5.0), so we can use a mean value: 4.8 kcal per liter of oxygen. Remember that metabolism is energy (units in kcal), but most experimenters, including ourselves, simply use Vo_2 as a measure of MR.

Vo_2 is the amount of oxygen consumed by the organism per unit time, specifically in biochemical reactions to make H_2O and CO_2. Similarly, Vco_2 is the amount of carbon dioxide produced by the organism in biochemical reactions, and then released into the environment.

Different types of food not only release different amounts of energy, but also release different amounts of carbon dioxide per oxygen molecule. This ratio is called the Respiratory Exchange Ratio (RER).

$$RER = Vco_2 / Vo_2$$

RER is 1.0 for carbohydrates, 0.7 for lipids, and 0.8 for proteins and for mixed diets. Note that RER indicates the kind of diet of the organism, and does not indicate its' metabolic rate (that is Vo_2 alone).