Mammalogy Lecture 17 – Thermoregulation/Water Balance

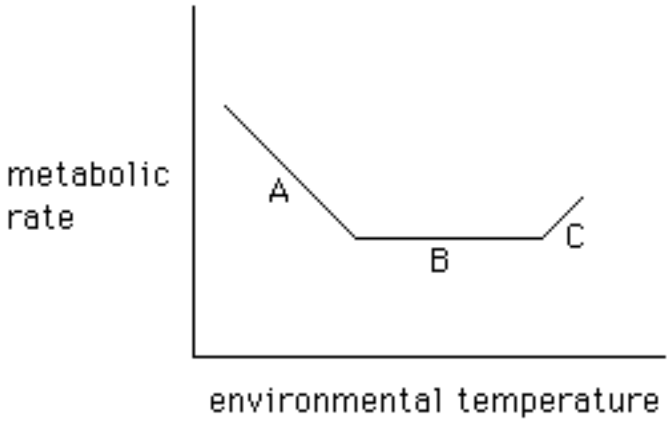
I. Introduction. Obviously, mammals are endotherms; they regulate body temperature via metabolic processes by burning energy.

For all endotherms, there is a **Thermal Neutral Zone**

When T_A is low, energy is expended to keep warm.

When T_A is high, energy is expended to keep cool

But for every endothermic species, there is a thermal neutral zone*, the range of ambient temperatures across which metabolic rate is at basal levels (that is, across which there's no increasing cost of homeothermy).



T_{LC} - highest temperature at which an endotherm expends energy to stay warm.
T_{UC} - lowest temperature at which an endotherm expends energy to stay cool.

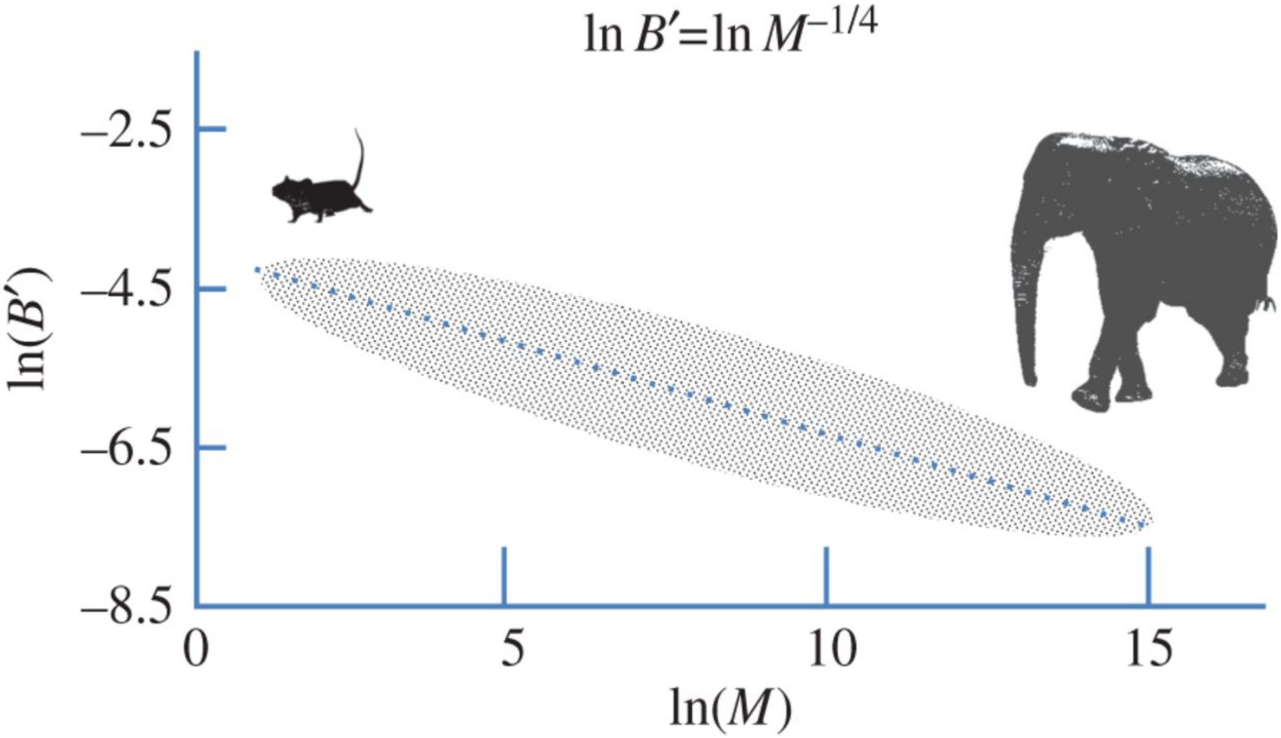
Obviously, when ambient temperatures are either below T_{LC} or above T_{UC}, there is a metabolic cost to homeothermy (maintaining a constant body temperature).

*The TNZ can shift to some degree in some species (Zhao et al. 2014), but not by a lot, and it's only been shown to expand to include cooler temperatures (Liao et al. 2022).

II. Adaptations for Cold – Temperatures in Zone A

A. Large Size – Relates back to S/V ratio and thermal inertia.

B. High Basal Metabolic Rate - Cold adapted species have a higher-than-expected basal metabolic rate.



For example, Red foxes, *Vulpes vulpes,* have a BMR that's nearly twice as high as similar sized canids in warmer regions.

C. Insulation -

Pelage - forms a barrier of warm air next to the surface of the animal.
Blubber - subcutaneous fat is commonly used as an insulating mechanism in marine mammals.

D. Regional Heterothermy

Extremities may be allowed to cool, sometimes to very low temperatures. This is accomplished by vasoconstriction.

Urocitellus paryii - toe pads may be 2° - 5° C
Ondatra zibethicus – extremities are allowed to cool to water temperature

E. Systemic Heterothermy – Adaptive Hypothermia

Characterized by:
- Decreased body temperature
- Decreased heart rate

- Vasoconstriction - severe reduction of blood flow to the extremities (i.e., regional heterothermy).
- Decreased breathing rate
- Suppression of shivering
- Decreased oxygen consumption (decreased metabolic rate)

There is usually great **energy savings** associated with hypothermia (especially for small mammals).

Maintenance of high T_B at very low temperatures is energetically costly and without adaptive hypothermia, many small mammals would be unable to persist in many cold localities.

The cost, however, is that recovery from adaptive hypothermia requires the metabolism of a **special type of fatty tissue: thermogenic fat or brown fat**. This differs from regular or white fat in many ways, two of these are that there's a very high concentration of mitochondria and very highly vascularized.

Once brown fat stores are depleted, the animal loses the ability to arouse from adaptive hypothermia. The finite nature of brown fat reserves represents an additional cost to the strategy of adaptive hypothermia: the risk of being unable to arouse from torpor.

Adaptive Hypothermia is Classified in Two Ways: Depth or Duration

1. Depth - may be shallow (Torpor) or deep (Hibernation).

   a. Shallow - T_B may only drop very slightly or may drop as much low as 15^0 C

   b. Deep - T_B may drop precipitously, as low as few degrees above ambient. In Great Basin pocket mice, *Perognathus parvus*, T_{body} drops to ca. 2-3^0C

2. Duration - may be Seasonal or Daily

   a. Seasonal - Tends to be deep but is not always. *Ursus* exhibit seasonal hypothermia, but it's not deep.

   Triggered by a variety of stimuli.
   - food limitation
   - photoperiod
   - may require a cold preparatory period of 6-8 weeks of cold temperature

   b. Daily - Follow a circadian rhythm

Usually only shallow. Only a slight decrease in T_B, breathing, & MR (e.g., *Peromyscus* & Kangaroo mice *Microdipodops*).

This capacity for daily torpor in *P. maniculatus* has been cited as critical adaptation that allows this otherwise very generalized mouse species to occupy such extremes habitats as boreal through desert habitats.

Temperate bat species of *Myotis* exhibit both daily and seasonal hypothermia

A common usage, which mammalogy texts often use, is that torpor is a very general term for any period of dormancy. Hibernation is deep torpor seen in the winter. Others use the terminology we used here, where torpor is restricted to shallow hypothermia and hibernation is deep hypothermia.

III. Strategies for Heat – Look back at TNZ curve, and focus on zone C.

Because mammals are endotherms, they are pre-adapted for dealing with cold. However, they are rather poorly prepared for dealing with heat.

A. The simplest way of dealing with heat is to **avoid exposure** to it.

1. Almost all desert rodents are **nocturnal** and therefore are active during the coolest part of the day.

2. Many desert species, especially rodents, are somewhat **fossorial**. They shelter in burrows throughout the day and burrow temperatures are as much as 35° C lower than surface.

3. Daily or Seasonal Dormancy: Long-term dormancy during the summer is called **estivation (aestivation)**.

Daily torpor in *Peromyscus eremicus* allows this otherwise generalized rodent to inhabit deserts.

B. For many desert mammals, avoiding exposure to heat is not an option, so they have to deal with it.

1. Typically have **lower BMR** than expected based on size, so less heat is generated.

For example, desert species of ground squirrels fall below the curve of metabolic rate on body size.

This is true for an Idaho species, *Urocitellus mollis*, and it’s true for *Xerospermophilus mohavensis*.

2. Large mammals can’t find the refuges that are available to small mammals.

Thus, especially African cetartiodactyls deal with hyperthermia, elevated T_{body}.

It then becomes necessary to protect vital organs from high temperatures.

The brain is the most sensitive organ.

African bovids have evolved countercurrent exchange mechanisms to **keep the brain cool**.

The carotid artery passes through a *rete mirabile*, a complex series of capillaries, which then supply the brain with blood.

Venous blood returning from the brain passes through the olfactory epithelium where it is cooled by evaporation of the mucous membranes in the nasal cavities.

This cooled venous blood enters the rete mirabile and the hyperthermic arterial blood in the carotid artery dumps its heat to the cool venous blood. This is the site of the counter-current heat exchange. This keeps the brain several degrees cooler than the core body temperature.

Perissodactyls lack this, and Mitchell and Lust (2008. Biol. Lett. 4:415) have proposed that this explains the high diversity of terrestrial cetartiodactyls.

C. The most universal method of dealing with heat involves **evaporative cooling**.

As water evaporates heat is absorbed by vapor- thus the surface off which the water evaporates is cooled.

a - The most common method - producing sweat.
b - Saliva - Many Macropodids, for example, moisten their forearms with saliva.
These regions are highly vascularized and vessels are dilated during heat stress. The evaporating saliva cools the venous blood in the extremities.
Many cervids do this as well.
c - Panting.
There is some effect by evaporation of saliva, but the major effect is derived from evaporation of moisture in the lungs, where blood is in close contact with surface tissues. **This is called pulmonary evaporation, which is a huge source of water loss.**

Evaporative cooling is the most effective.

IV. Water Balance

Water loss is obligatory. The strategy for desert-adapted mammals is to try to minimize loss.

A. Loss Occurs Via

1. Evaporation from body via sweat: cutaneous evaporation.

2. Evaporation from respiratory system, including lungs and mucous membranes: pulmonary evaporation.

3. Waste, both in urine and feces

4. Lactation - This is a huge cost to the water budget of reproductive females. In desert-adapted forms, maternal females recover some of the water invested into milk production by ingestion of offspring's feces and urine, but just a portion of it.

B. Sources of Water

1. Drink Free Water - Water that is freely available in the desert is very rare. Consequently, many desert-adapted rodents have lost the ability to drink free water.

2. Preformed (Dietary) Water - Water in tissues of food.

   Herbaceous plants are high in water content and therefore are selectively eaten.

   In addition, many plants are hygroscopic. They take up water during the evenings when there is a little more moisture.

   Many desert rodents such as *Neotoma lepida* feed on *Opuntia* cactus.

   Carnivorous desert mammals obtain all the water they require from their prey.
   Onychomys leucogaster
   Taxidea taxus
   Vulpes macrotis,

3. Metabolic Water - Formed as a by-product of oxidation.

   The amount of metabolic water produced depends on both the amount of food eaten and the composition of the diet.

   Metabolism of protein -- 0.396 g H_20/g food
   carbohydrate -- 0.556 g H_20/g food

fat -- 1.071 g H_20/g food

We might expect desert species to eat lots of fatty foods, but they tend not to because of the high energetic cost of metabolizing lipids. It's more efficient to eat a lot of carbohydrates.

Many desert rodents rely exclusively on metabolic water production.

For those species (for example, Heteromyids) -

Higher the metabolic rate, the more metabolic water produced.
But, the higher metabolic rate, the higher the heat production.

There is a trade-off between water production via metabolic processes and heat stress.

These aspects of an animal's water budget must balance; for the most part, losses = gains.

But, in general, desert adapted species can tolerate much higher levels of dehydration than generalized mammals.

In *Homo* and *Rattus*, loss 10-15 % of body weight leads to death.
Camels fully exposed to desert sun lose 25 % or more of body weight in water.

Strategies for Conservation of Water

Obviously, some of the same strategies for avoiding heat stress will also result in water conservation by eliminating the need for evaporative cooling.

1. Nocturnal - not only avoid the need for evaporative cooling, but many forms feed only at night. This is the most humid part of the day and leaves absorb moisture from the relatively humid night air. This is critical to *Oryx gazella* (gemsbok) in Kalihari desert.

2. Fossorial - We've discussed the fact that it's cooler in burrows than on the surface.

   In addition, many desert rodents plug their burrows. Plugged burrows trap respired moisture and the relative humidity in burrows is up to **76%** relative humidity, much higher than outside.

   Dry seeds are usually stored in humid burrows, where they absorb respired moisture from the air.

   This absorbed water may account for up to 30% of a kangaroo rat's daily water requirement.

3. Nasal Recycling - Critical to the water budget of desert rodents.

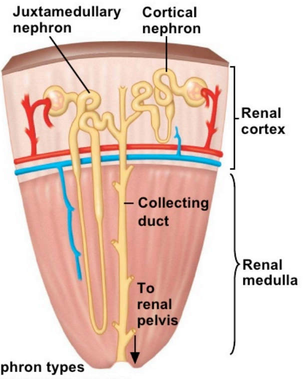
- Exhaled air is cooler than body temperature in these forms.
- They have a long, narrow rostrum with large nasal mucosa, the membrane that produces nasal mucus.
- As air is inhaled, cools the mucosa: slight amount of evaporative cooling
- Once in the lungs, air becomes warmed to body temperature and saturated with water.
- On exhalation, this warm moist air passes the cool mucosa.
- This cools the air and the moisture from pulmonary evaporation condenses.
- Much of this is absorbed through the mucosa.

With this strategy, *Dipodomys* recover 80% of their pulmonary evaporation.

Some evidence that Giraffes also recycles water this way.

4. Concentrate urine - All desert species have this ability to some degree.

The mammalian characteristic of excreting nitrogenous waste as urea preadapts mammals for the production of concentrated urine.



(c) Nephron types

Review, the nephron is the unit of the excretory system

Renal capsule - Glomerulus/Bowman's capsue

Loop of Henle - very long Loops of Henle - permit a great deal of resorption of water and therefore the production of concentrated urine.

All mammals have a mixture of nephrons with long and short loops of Henle.

In desert-adapted rodents, the long Loops of Henle are relatively longer than in generalized mammals. In addition, a higher percentage of nephrons have these very long loops of Henle. During heat stress, vasoconstriction in the afferent redirects blood only to these nephrons. In *Dipodomys*, the urine may have 11 times the osmotic pressure as the plasma.

This layout allows phenomenal flexibility, perhaps best exemplified by Vampire bat *Desmodus rotundus* (e.g., Busch. 1988. Comp. Biochem. & Physiol. A., 90:141).

As we've discussed, vampire bats are sanguinivorous and have lots of cool adaptations: blade-like incisors, saliva containing anesthetics, anticoagulants and (recently discovered), vasodilators (Kakumanu et al. 2019). A single blood meal may be as much as 60% of their body weight in blood. Therefore, a 35 - 40 g bat ingests a blood meal of about 18 - 22 g (in ~ 10 – 30 minutes).

These animals begin to urinate immediately after they begin to feed (peak urine flow occurs about 20 minutes after start of feeding). Initially, the urine that is produced is very dilute. The effect is to leave cellular components of the blood in the g.i. tract.

This results in less risk of predation than would be the case were they flying back to the roost carrying the full weight of their meal.

Once back at the roost, they have absolutely the opposite situation. They have a very nitrogen rich food, but they're in a state of very low hydration because they have just produced copious dilute urine.

By increasing the blood flow to the nephrons with very long Loops of Henle, they are able to switch their renal physiology 180°, and produce very concentrated urine, as highly concentrated as *Dipodomys*.