Mammalogy Lecture 14 - Thermoregulation/Water Balance

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

A. Ectotherms -- T_b proportional to T_A

Metabolic rate is directly proportional to ambient temperature.

\[ \frac{O_2 \text{ Consumption}}{T_A} \]

B. The situation is very different with endotherms.

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.

\[ \frac{O_2 \text{ Consumption}}{T_A} \]

TLC – (lower critical temperature) highest temperature at which an endotherm expends energy to stay warm

TUC – (upper critical temperature) lowest temperature at which an endotherm expends energy to stay cool

Obviously, when ambient temperatures are either below TLC or above TUC, there is a metabolic cost to homeothermy - maintaining a constant body temperature.

Many mammals minimize this cost by allowing their body temperature to either drop or increase.

May be seasonal or daily

II. Adaptations for cold
A. Large Size - Size is critical because of the relationship between body size, S/V and cooling.

Remember that heat loss is directly related to S/V ratio - small animals cool faster.

In general, more northerly species are larger than southerly species.

This also typically holds true within a species. - Bergman’s Rule
Arctic wolves are larger than populations in more temperate regions.
Alaskan Moose are larger than those from more moderate localities.

There are notable exceptions -- *Peromyscus* body size is inversely correlated with latitude.

Almost all marine mammals are very large; cold is more of a problem in water because water has much higher thermal conductance than air.

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

<table>
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<tr>
<th>Basal Metabolic Rate</th>
<th>O₂ consumption/hour/gram</th>
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Body Weight

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

C. Insulation - Extra layers to reduce heat loss
- obvious one is pelage - forms an barrier of warm air next to the surface
- Many artiodactyls have hollow hair - hollow hair is a better insulator than solid hair

- 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.

*Canis lupus* - toe pads may be 0°

*Spermophilus paryii* - toe pads may be 2° - 5° C

Particularly true for aquatic and semi aquatic mammals.

Muskrats *Ondatra zibethicus* - Vasoconstriction occurs in limbs and the temperature of the limbs is allowed to drop to the ambient water temperature.

E. Systemic Heterothermy – Adaptive Hypothermia

Many mammals deal with cold via Adaptive Hypothermia - Allow \( T_b \) to Drop

Seen all three major groups of mammals - Monotremes

- Marsupials
- Insectivora, Chiroptera, Primates, Carnivora, Rodentia.

Thus, it has evolved many times.

Characterized by:
- Decreased heart rate
- Vasoconstriction - severe reduction of blood flow to the extremities
- Decreased breathing rate
- Suppression of shivering
- Decreased oxygen consumption (decreased metabolic rate)
- Decreased body temperature

There is usually great **energy savings** associated with hypothermia –

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 looses 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.

Classify Adaptive Hypothermia two ways.

1. May be shallow (Torpor) or deep (Hibernation).
   a. Shallow - \( T_b \) may only drop very slightly or may drop as much low as 15°C
   b. Deep - \( T_b \) may drop precipitously --- As low as few degrees above ambient. Great Basin pocket mouse *Perognathus parvus* - temperature drops to ca. 2-3°C

2. May be Seasonal or Daily
   a. Seasonal - long term
      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
      (I’ll give an example of this in a minute.)
   b. Daily - Follow a circadian rhythm
      Usually only shallow. Only a slight decrease in \( T_b \), breathing, & MR *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.
      Daily torpor is more common in small mammals, it’s not restricted to small mammals. For example American badger, *Taxidae taxus*, enters short-term torpor frequently during the winter.
      Heart rate is cut in half from 55 to 25.
      Body temperatures drop around 10°C to 29°C
Responses to cold are particularly interesting in many temperate bat species *Myotis*.

They exhibit both daily and seasonal hypothermia

During the summer, there is no daily torpor, bats are homeothermic - some storage of brown fat occurs.

As fall progresses, bats utilize a **preparatory period**. They enter shallow torpor at their roosts during the day; metabolic rate drops by a factor of 10.

This allows for much more rapid accumulation of brown fat.

Bats actually increase fat storage without increasing the rate of food intake!

Spend the winter in deep hibernation & arouse a few times to eliminate waste.

Each arousal requires the metabolism of brown fat.

They require extremely precise microclimate requirements & are very sensitive to brief warming, even to the point that a few biologists standing under a group of hibernating bats can raise the ambient temperature enough to initiate arousal.

If you go into a bat hibernaculum, you’ll often see a few bats that never made it out of hibernation. Their carcasses remain hanging and actually tend to mummify.

Before we leave this, there are two sets of terminology.

Your book uses Torpor as a very general term for any period of dormancy. Hibernation is deep torpor seen in the winter. Others use the terminology we used here. Topor is restricted to shallow dormancy and hibernation is deep hypothermia.

III. Strategies for Heat – Look back at TNZ curve

A. Because mammals are endotherms, they are really pre-adapted for dealing with cold. They are actually rather poorly prepared for dealing with heat.

B. The most universal way of dealing with heat is to avoid exposure to it.
1. Almost all desert rodents are nocturnal - active during the coolest part of the day.

2. Many desert species, especially rodents, are somewhat fossorial - shelter in burrows throughout the day.

   In deserts, because of the aridity, there is a rapid radiational cooling of the ground at night.

   The ground retains only 10% of the solar radiation absorbed during the day, as opposed to 60% retained in non-desert environments.

   Soil temperatures are much cooler than surface temperatures.

   *Dipodomys mirriami* burrows are 0.5 - 1.5 meters below the surface.

   When the surface temperatures reach 70°C
   \[ T_{0.5} = 480 \text{°C} \quad T_{1.5} = 350 \text{°C} \]

3. Daily or Seasonal Dormancy: Long term torpor during the summer is called estivation.

   Daily torpor in *Peromyscus eremicus* allows this rather generalized rodent to inhabits deserts.

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

1. Typically have lower basal metabolic rates than expected just based on size -- less heat generated.

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

2. Pelage characteristics:

   Coats are often glossy to reflect solar radiation

   Distribution of Fur:
   - Usually thick on the dorsal surface. This serves as insulation from the sun.
   - usually very thin on the under surface. This allows heat to be dumped to the shaded ground.
This is especially important to Hyraxes - *Procavia* These African mammals spend the warm afternoons with their venters pressed against cool shaded rocks. The thin ventral pelage allows from more efficient cooling than would be possible with dense ventral pelage.

3. Miscellaneous morphological adaptations – Shade & Radiators

   a. Species of *Ammospermophilus* are active throughout the day in deserts and use their tail as a parasol.

   b. Many mammals have highly vascularized membranes that are used to dissipate excess body heat. *Lepus californicus* rests in the shade during the day and the blood vessels in the ears are fully dilated.

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

   As water evaporates heat is absorbed - thus the surface of which the water evaporates is cooled.

   a - The most common method - producing sweat.

   b - 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.

   c - Saliva -- For example, many Macropodids 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.

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

   As a result many, especially African Bovids deal with hyperthermia, elevated $T_{body}$

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

   The brain is the most sensitive organ.

   Many african bovids have evolved countercurrent exchange mechanisms to cool keep the brain cool.

   The carotid artery passes through a Rete Mirabile - complex series of capillaries.
Venous blood returning from the brain passes through capillaries in 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.

So, of all these mechanisms for dealing with heat, evaporative cooling is perhaps most effective.

Problem: For desert organisms, this is the most costly mechanism in terms of water balance.

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 Urine and feces

4. Lactation - This is actually a huge cost to the water budget of reproductive females. In desert adapted forms, much of the water invested into milk production is recovered by the mother by ingestion of offspring’s feces and urine.

B. Sources of Water

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

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

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

   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 velox*

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

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

Metabolism of protein -- 0.396 g H₂O/g food  
Carbohydrate -- 0.556 g H₂O/g food  
Fat -- 1.071 g H₂O/g food

We might expect desert species to eat lots of fatty foods, but they actually tend not to because of the high energy 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 - 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.

*Homo* and *Rattus* - loss 10-14% of body weight leads to death.  
Camels fully exposed to desert sun loose 25% or more of body weight in water.

C. 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 form the relatively humid night air.

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. This traps 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 actually absorb respired moisture from the air.

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

3. Sweat prevention - obligate - many desert rodents don’t actually sweat
   - facultative - many bovids repress sweating when water-stressed.

4. Shifts in diet -
   *Ammospermophilus* shifts diet seasonally - feed on more carbohydrate-rich foods in the dry season to optimize production of metabolic water. They also tend to feed on insects, which are a good source of preformed water.

   - Exhaled air is actually cooler than body temperature in these forms
   - long, narrow rostrum with large mucosa - membrane that produces nasal mucous
   - 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 the pulmonary evaporation.

Some evidence that Giraffes also recycles water this way.

6. Dry feces - produce fecal pellets ---> Great deal of resorption of water from feces in large intestine.

*Dipodomys* loses about 5.5 times less water in feces than *Rattus*

7. Concentrate urine - All desert species have this ability to some degree.
Actually the mammalian characteristic of excreting nitrogenous waste as urea preadapts mammals for the production of concentrated urine.

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 re directs blood only to these nephrons. -- In Dipodomys, the urine may have 11 times the osmotic pressure as the plasma.

This layout actually allows phenomenal flexibility, as exemplified by Vampire bat Desmodus rotundus

As the common name implies, vampire bats feed on blood - can ingest 50% of their body weight in blood. Therefore, a 34 g bat ingest a blood meal of about 18 g.

These animals begin to urinate immediately after they begin to feed. 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 produces
By increasing the blood flow to the nephrons with very long Loops of Helne, they are able to switch their renal physiology 180°, and produce very concentrated urine, as highly concentrated as *Dipodomys*. 