Winter Ecology – Mammals in Winter

Objectives – ***See Review Questions and Field & Lab Exercises at end of handout)***

- Identify Rocky Mountain mammals likely to be present in the environs of the MRS, and describe natural history as it relates to winter ecology of various groups of mammals.
- Describe 3 different kinds, each, of morphological, physiological, and behavioral adaptations to living in the cold.
- Describe the importance of attributes of snow, vegetation, and landform to survival of mammals in winter.
- Identify and distinguish mammal sign among families of mammals.

Boreal Ecology: *Vertebrate adaptations to cold*
Adapted from: *Marchand, P.J. 1996. Life in the cold: an introduction to winter ecology. University Press of New England, Hanover, NH*

- Options for animals getting through the winter:
  - Migration
  - Hibernation
  - Resistance
- Basics of energy exchange
  - Conduction
  - Convection
  - Radiation
  - Latent heat of exchange
- Warm bodies in cold environments
  - Morphological vs physiological thermoregulation
  - The problem with appendages

Options for animals getting through the winter:
1. Migration 2. Hibernation 3. Resistance

1. Migration
May seem like a logical alternative to wintering in the Boreal region, BUT

- energetic costs of traveling long distances is high
  - Primarily birds migrate
  - It is estimated that a mammal would expend approximately 10 times more energy moving a given distance than a bird of equivalent weight
  - There are exceptions: e.g., caribou

2. Hibernation
If can't migrate, hibernate to avoid food scarcity and extreme cold

- True hibernators are *homeotherms* (warm-blooded mammals; NOT birds) that can periodically enter state of reduced metabolic activity, allowing body temperature to fall many degrees below normal without any ill effects
  - Requires animals to survive for period of time on finite energy reserves (stored fat or food)
  - Reserves must be enough for:
    - Maintenance of life functions such as respiration
    - Periodic arousals (as often as once every few days) and rewarming during winter

- Can still have high mortality during particularly hard winters:
  - e.g., small mammals (mice [*Peromyscus* sp.], ground squirrels [*Citellus* sp.]):
    - 23-68% mortality for adults
    - 41-93% mortality for juveniles

- Safety of hibernating animal may be limited by availability of den sites where temperatures not likely to drop significantly below freezing

3. Resistance
Birds and mammals that remain active throughout winter face a special problem:

- They must maintain a body temperature within narrow and relatively high limits
- Must produce enough metabolic heat from food or fat reserves to offset that lost to cold surroundings

How modes of energy transfer are important to animals wintering in the north:

- Conduction
- Convection
- Radiation
- Latent heat exchange

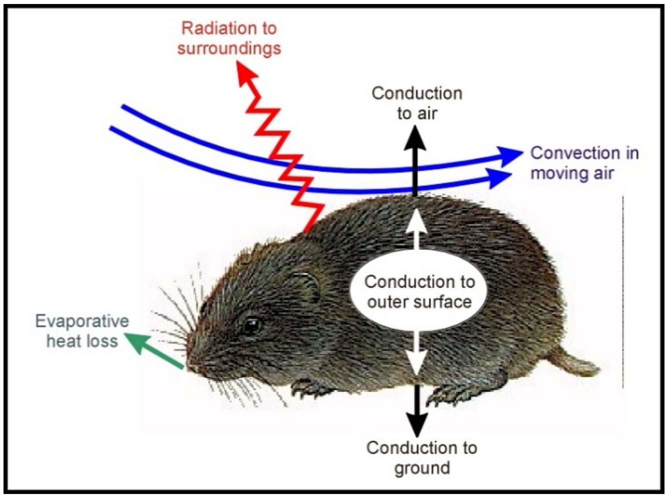

FIGURE: Heat loss from a small homeotherm. The total amount of heat lost from an animal's skin, fur, or feathers, by conduction, convection, and radiation is equal to the amount of heat conducted from the animal's core to the outside of its body. Thus, heat loss in winter can be approximated by using a model for conduction alone, where it is necessary to know only the thickness and thermal conductivity of the animal's insulation, its surface area of exposure, and the temperature difference between the animal's core and its surroundings. Latent heat loss by evaporation is assumed to be negligible at this time of year

Basics of energy exchange:
Conduction:

- Energy transfer through molecular collision
- Must have contact between media involved in heat transfer (e.g., skin and air, feet and ground)
- Therefore, amount of conduction dependant on:
  - surface area of exposure
  - efficiency of heat transfer through conducting media (high density materials have high thermal conductivity; because layer of fur or feathers is not solid, there is little thermal conductance)
  - temperature difference between 2 medias (the greater the temperature difference, the greater the conductance)

Thermal conductance can be mathematically modeled:

$$Q_c = kA\frac{(T_b - T_a)}{d}$$

Where:
k = thermal conductivity (in W/cm °K)
A = surface area of exposure (in cm^2)
$T_b - T_a$ = temperature gradient between animal's core (T_b) and outside air (T_a) (in °C or °K)
d = distance between core and outside air (in cms)
Qc = total heat loss (in watts)

Convection: Transfer of energy via a *moving* fluid, especially air or water

- Both total area exposed to the moving fluid, and temperature difference between surface of object and fluid are important in determining total heat loss.

- Thickness of boundary layer enveloping object, which is influenced by:
    - Size and shape of object
    - Surface roughness
    - Wind speed

Equation describing convection is similar to that for conduction:
k = thermal conductivity of air or water
d = thickness of the boundary layer across which the temperature difference between surface and surroundings is measured

Radiation: Propagation of energy through space
Two properties that determine amount of energy radiated:

- Temperature (independent of ambient temp)
- Characteristic efficiency of radiant energy transfer, termed emissivity

An object whose temperature is above absolute zero radiates energy in direct proportion to its temp, with most natural objects emitting radiant energy at an efficiency of between 90-99% of the maximum possible for their temps
Can calculate total energy loss via radiation using:

$$Q = \varepsilon\sigma T^4$$

Where:
Q = total energy lost
ε = objects emissivity
σ = Stefan-Boltzmann constant (5.67×10^{-8} W/m^2 ^{o}K^4)
T = temperature of object (in ^{o}C or ^{o}K)

For homeotherms:

- Heat loss by radiation remains fairly constant throughout the year since body temperature varies only slightly over time

Using same equation, can also calculate heat gained by an animal through absorption of radiant energy emitted by its surroundings

Latent heat exchange: Amount of heat energy either tied up or liberated with phase changes of water

- e.g., conversion of 1 g of ice at 0^{o}C to water at same temperature requires addition of 335 joules of energy
    - when reverse process occurs, same amount of heat is liberated
- This means that it is important in winter to reduce evaporative heat loss, including heat loss associated with respiration

Warm Bodies in Cold Environments
Physical versus physiological thermoregulation
How much metabolic energy must be produced to offset total heat loss during winter?

- Heat in = heat out
    - Heat in from metabolism of food or fat, and energy absorbed from external sources (e.g., sunlight)
    - Heat out from combining equations for conduction, convection, radiation, and latent heat exchange

Assumptions:

1. Latent heat exchange is small in most homeotherms in winter (<10% of energy loss)
2. Total heat loss from outer surface of skin, fur, or feathers by conduction, convection, and radiation is equal to that which is *conducted from the core of the animal to the outside surface*

Because heat can't be stored on the surface of an animal, no matter how heat is lost from the surface via conduction, convection, radiation, the total equals amount conducted through insulating layers from core of animal

Therefore, if we assume that metabolic heat is only substantial heat input, an animals energy (heat) budget can be represented by:

$$M = kA\frac{(T_b - T_a)}{d}$$

Where:

M = heat produced by metabolism *(See earlier for other terms!)*

The model tells us there are several ways the animal can maintain constant metabolic rate
As air temperature drops and $t_b - t_a$ increases, metabolism can be held constant by:

- Decreasing thermal conductivity (k)
- Decreasing surface area exposed (A); e.g., curling up and retracting extremities, huddling with other animals
- Increasing thickness of insulating layer (d); e.g., erection of hairs or fluffing of feathers (trapping air).

THE ENERGETIC ADVANTAGE OF HUDDLING

Because heat loss by conduction or convection varies in direct proportion to the amount of surface area exposed by the animal, the energy savings of huddling can be calculated easily. In the case of the small mammals pictured above, assume the following:

- Their effective surface area without huddling is 53.5 cm^2
- The thickness of their insulation (fat, skin, and fur) is 0.5 cm
- The thermal conductivity of their insulation is 0.004 W/cm/°K
- Their body core temperature is 37.5 °C while the temperature of their surroundings is –20°C
- Their respiratory heat losses are negligible

Heat loss by conduction may now be calculated as follows:

$$Q_c = kA\frac{(T_b - T_a)}{d} = (0.004 \times 53.5 \times 57.5/0.5) = 24.61 \text{ joules/sec (or 24.61 watts)}$$

Now assume that by huddling each animal reduces its surface area of exposure by one-third. Their heat loss would then be reduced by an equal amount, as follows:

$$Q_c = (0.004 \times 35.68 \times 57.5/0.5) = 16.41 \text{ joules/sec}$$

In this same manner, the energetic advantage of nest building may be calculated by accounting for the effect of the nest on the $T_b - T_a$, the body-to-air temperature difference, or by adding the thermal conductivity and thickness of the nest materials to the k and d terms, respectively.

Can also try and elevate air temperature through microclimate modification:

- e.g., nest building or going below ground.

Reducing body temperature also has same results:

- e.g., some animals like birds may undergo nightly torpor or controlled hypothermia, reducing body temperature a few degrees

Many small mammals that are solitary during summer become social in winter, constructing communal nests under snowpack, or in trees:

TABLE: Non-colonial small mammals that may congregate during winter.

Common name(s)	Scientific name
Boreal redback vole	*Clethrionomys gapperi*
Red Squirrel (Chickaree)	*Tamiasciurus hudsonicus*
Least shrew	*Cryptotis parva*
Mountain vole	*Microtus montanus*
Prairie vole	*Clethrionomys gapperi*
Meadow vole	*Microtus pennsylvanicus*
Pine vole	*Microtus pinetorum*
White-footed mouse	*Peromyscus leucopus*
Deer mouse	*Peromyscus maniculatus*

- e.g., a beaver lodge in winter occupied by 2 or more animals, remains well above freezing inside central chamber

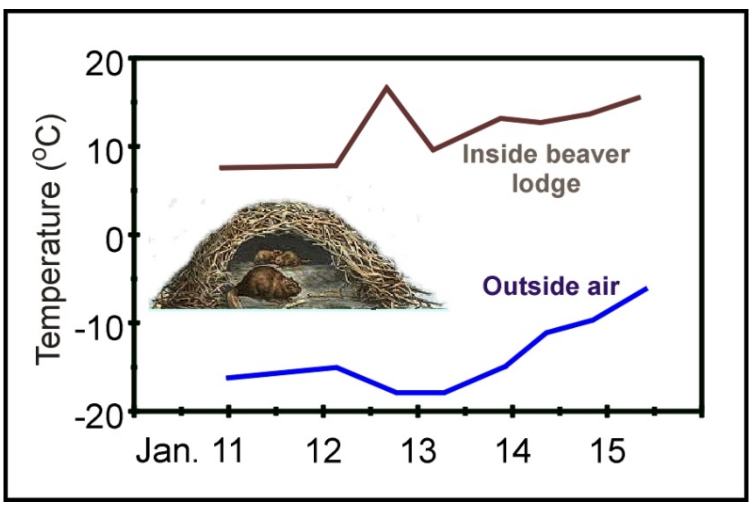

FIGURE: The ultimate communal nest. The inside of a snow-covered beaver lodge may be as much as 35°C warmer than the outside air in mid winter. This lodge was occupied by at least two adult beavers and was monitored by means of a thermistor probe inserted through the lodge wall and into the central chamber.

- Nests of 5-10 taiga voles have been found to be between 7-12°C warmer than ground temps, and as much as 25°C warmer than air temperatures above snow
  - Nest never completely vacated so foraging animals return to warm nest
  - might also help in slight reduction of water loss as high relative humidity in nest chamber reduces evaporation and reduced latent heat loss

At some point, animal must increase metabolic rate to balance heat loss

- Temperature at which this becomes necessary is termed the *lower critical temperature* (LCT)

Lower Critical Temperature:
Some small mammals lower LCT slightly during winter by seasonal increase in basal metabolic rate

- Varies amongst species
- Seasonally adjusted in many animals
- e.g., red fox lowers LCT from 8^{o}C in summer to –13^{o}C in winter, primarily through increased thickness of undercoat.
- Helps counter small heat loss before having to elevate metabolism to balance heat budget

Below LCT, physiological thermoregulation takes over:

- Increased ability for "non-shivering thermoregulation **(NST)**" heat production has been seen during acclimatization to cold in many small mammals
- e.g., increase in brown fat deposits - Brown Adipose Tissue **(BAT)**, close to the vital organs
    - brown fat has greater number mitochondria, and thus capable of higher rate of O_2 consumption and heat produced than white fat
    - secretion of hormone nor-adrenelin from adrenal medulla due to cold stimulates heat production in brown fat
    - e.g., in red-backed voles: increase in brown fat begins in early fall and continues into winter, changes cued by decreasing day length and low temps

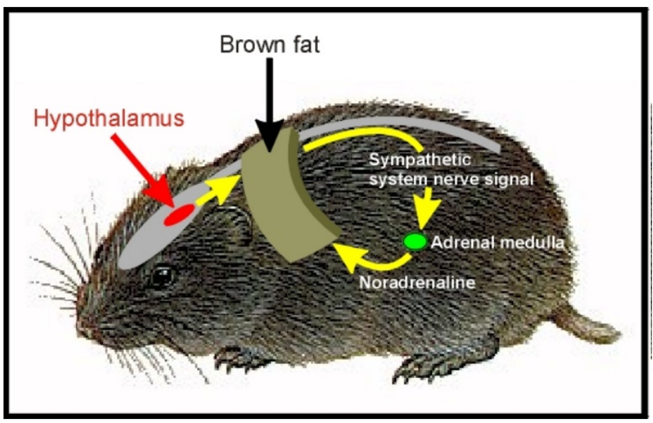

FIGURE: Heat on demand from brown fat. Brown fat may be likened to a heating pad. As depicted, a nerve signal sent from the hypothalamus in the brain (the thermostat) to the adrenal medulla triggers the secretion of nor-adrenaline directly into the blood stream. It is this hormone that apparently stimulates rapid heat production in the mitochondria-rich brown fat tissue, which is usually concentrated in the inter-scapular region, close to the vital organs.
Shivering eventually takes over if all else fails

- Heat production by involuntary shivering is last resort

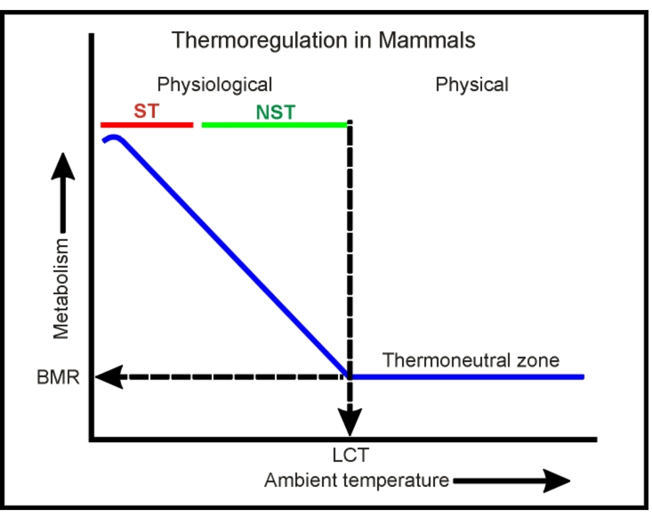

FIGURE: Physical versus physiological temperature regulation. Within the thermo-neutral zone, the animal's resting or basal metabolic rate (BMR) is relatively constant, maintained through physical adjustment of surface area and conductivity, such as changing posture or by huddling. As air temperature decreases and the limit of physical thermoregulation is surpassed, a point designated as the lower critical temperature (LCT), metabolic rate and consequent heat production increases. In most mammals this stepped-up heat production is accomplished first through non-shivering thermogenesis (NST), which involves the metabolism of brown fat, and then, as a last resort, through shivering or increased muscle activity – Shivering Thermogenesis (ST). In birds the LCT is without clear definition. Instead, there is a more gradual shift from physical to physiological thermoregulation, with increased heat production below about 30^{o}C accomplished entirely by shivering.

TABLE: A number of thermoregulatory strategies are employed by winter-active homeotherms to achieve the same results – maintenance of body temperature when the ambient temperature drops. The table below is a compilation from the literature on the given species

	Common shrew (*Sorex araneus*)	Redback vole (*Clethrionomys gapperi*)	Prairie vole (*Microtus ochrogasteri*)	White-footed mouse (*Peromyscus leucopus*)	Long-Tailed Weasel (*Mustela frenata*)	Snowshoe Hare	American Pika	Red Squirrel (*Tamiasciurus hudsonicus*)	Beaver (*Castor canadensis*)	Whitetail deer (*Odocoileus hemionus*)
Morphological & Behavioral										
Increased insulation	+			+	+				+	+
Subnivean	+	+	+		+				+	
Community nesting		+	+	+					+	
Physiological										
Torpor			No	+	No	No	No	+	**+**	
Adjusted BMR	+↑	+↑	+↑	+↑	No		+	No		+↓
Increased NST capacity	+	+	+	+	No		+ (only in fall)	No		?
Increased ST capacity		+			No			+	**+**	+
Weight adjustment	+↓	+↓	+↓	No	No		+↓		+↓	+↓
Countercurrent heat exchange					No			No	+	

\+ – Known winter adaptation
? – likely, but evidence is inconclusive
Blank – not reported in the literature for a given species
No – known not to occur

The problem with appendages
If homeotherms didn't need legs for getting around, they would be much better off without them in winter:

- Must be supplied with O_2 and kept from freezing by circulating blood through them
  - BUT must also avoid excessive heat loss
- Counter current system of blood flow (see diagram)
  - When air temperatures become low enough, superficial veins in extremities constrict, increasing flow resistance, shunting more blood through deeper veins lying close to arteries

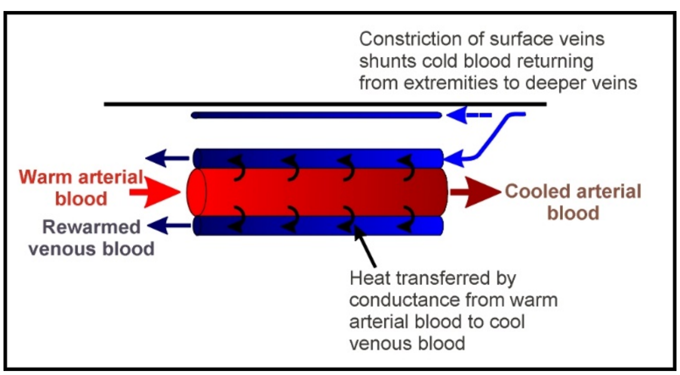

FIGURE: Countercurrent heat exchange. Warm arterial blood gives up its heat to cold blood returning from the extremities through veins lying in close contact with the arteries. Thus, the flow of heat, not blood, is short-circuited – arterial blood is pre-cooled on its way out and venous blood pre-warmed on its way back. This system of heat exchange is particularly well developed in the legs of birds, where a dense network of veins surrounds the central artery. Beavers, and otters also use countercurrent exchange in their tails.

Resources and References:

Armstrong, David M. 1987. *Rocky Mountain Mammals*. Univ Press of Colorado, Boulder, Colorado. 223 p.

Elbroch, Mark. 2003. *Mammal Tracks & Sign: A Guide to North American Species***.** Stackpole Books, Mechanicsburg, PA. 778 pages.

Halfpenny, James C. and Elizabeth A. Beisiot. 1986. *Field Guide to Mammal Tracking in North America*. Johnson Printing, Boulder, Colorado.

Rezendez, Paul. 1999. *Tracking and the Art of Seeing 2e : How to Read Animal Tracks and Sign Harper* Collins, NY, NY.

Taylor, Cathy A. and Martin G. Raphael. 1988. Identification of mammal tracks from sooted track stations in the Pacific Northwest. Reprint from Calif. Fish & Game. 74(1):4-15 http://www.fs.fed.us/psw/publications/4251/taylor1.pdf

Weir, RD., F. Corbould and A.S. Harestad. (2004) Effect of ambient temperature on the selection of rest structures by Fishers. pp. 187-197 in Gilbert Proulx, Angela K. Fuller, Daniel J. Harrison, editors. *Martens and fishers (Martes), in human-altered environments: An international perspective.* Springer, New York. 279 pages.

Fishers, like American Martens, choose rest structures based on ambient temperature, snow depth, and high wind speed. Fishers in Maine, Idaho, Connecticut – and this study – in Williston, B.C., choose rest structures (micro-habitats) based on thermal attributes of branch, cavity, and CWD (Coarse Woody Debris – subnivean) structures.

The Ecology of Fear: Scientists Say Wolves Are Helping Restore Yellowstone's Ecosystem
by Jeff Welsch for eMagazine online https://emagazine.com/the-ecology-of-fear/

Winter Adaptations of Mammals, includes species specific adaptations:
http://www.bobpickett.org/winter_adaptations.htm

Colorado Natural Heritage Program: Mammals
https://cnhp.colostate.edu/ourdata//trackinglist/custom-tracking/?group=6

Database of species, dedicated to preserving biodiversity and cataloging rare and endangered species
https://www.natureserve.org/access-data

Wildwood Tracking
https://www.wildwoodtracking.com/

Rocky Mountain Nature Association – Field seminars in Rocky Mountain National Park
https://rmconservancy.org/learn-with-us/field-institute/

Tracker, Ecotourist Guide, and Naturalist certification Resources
https://cybertracker.org/

Yellowstone Forever field courses
https://www.yellowstone.org/experience/field-seminars/

Review Questions and Terms to Know:
Define:

LCT	BAT
ST	Fossorial
NST	Habitat Island
Subnivean	Keystone Species
Torpor	Countercurrent heat exchange

Why is huddling an effective mechanism? Hint: surface area, and name 3 species that practice it.

If being compact and round like a pika is an effective winter thermoregulatory mechanism, then what mechanisms are used by long, thin weasels?

Does Delayed Implantation serve as a *Winter* survival strategy?

What 2 additional functions does a beaver's tail perform in the winter?

Some mammals *lose* weight in the winter. What is the proposed theory to explain that phenomenon?

Some areas of Colorado are at a 30 year low for snowpack this winter. In a low snow year, which mammals will thrive and which will likely perish?   Why?

Which times of the year are most dangerous for subnivean animals, and why?

Shrews have a very high BMR (Basal Metabolic Rate). Some species must eat every 2 or 3 hours. How does such a small mammal thermoregulate in the winter?

Name 3 species of mammals that hibernate.

In some areas, global warming has produced a "creep" upwards in elevation of boreal forest trees. Explain what this could mean for the pika. Hint: Refer to Chad's powerpoint presentation from Winter Ecology, 2005.

Are wolves and lynx keystone species? Make an argument for why or why not.

Mammal Field and Lab Exercises

Before Field Exercise:

1. Determine which species we are likely to see or detect sign at Niwot Ridge, MRS Elevation

2. Determine which species are here, but we are NOT likely to see sign.

3. Match foot casts and molds to the correct species, and become familiar with sizes of tracks, types of tracks (refer to key handout showing: 2, 3, 4, 5 toed, and gait charts)

4. Prepare a field chart to record possible species' sign:
i.e., WHICH habitat patch is a likely candidate for WHICH species. Your field notebook will be useful here.

We'll visit riparian areas with willows, alder, open stream, and lodgepole pine forest. Consider that some species prefer, or will cross open areas and "edges", while others prefer closed canopy interior forest.

After Field Exercise, consider the mammal specimens displayed:

1. Pick a mammal from each of the six orders displayed: Insectivora, Chiroptera, Rodentia, Lagomorpha, Carnivora, Artiodactyla. For each species you chose, research and write one strategy that species employs in each of the following Three categories: Behavioral, Morphological, Physiological.

Use this handout, online resources (Bobpickett.org article is especially informative), your texts, and any of the reference books and articles.

2. Take the Brian Booth's Tracking Quizzes – choose the ones labeled "snow" Remember to use ALL the clues!: https://www.trackingquiz.com/quiz/

3. Answer the review questions.