Endothermy: developmental aspects

Some small mammals are born relatively naked, uncoordinated, and helpless and are dependent on their parents for a long time (= *altricial development*)

Other species are more developmentally advanced, and show *precocial development*; they are typically furred at birth (or soon after), their eyes typically open soon, etc.

These categories are not monolithic—think of them as more of a continuum. Some animals can be altricial in some aspects and precocial in others.

All living reptiles are classified as precocial; this suggests that that is the ancestral state. The advantages are easy to see: young are able to move, fend for themselves, and escape predators quickly after birth (increases chances for survival)

Why, then, would altriciality develop?

Endothermy: developmental aspects

There are many hypotheses, but it is possible that altriciality is a 'byproduct' of being small: if you are small, your offspring must be *very* small, and consequently less well developed.

This would make altriciality a necessity, and possibly nonadaptive.

However, there are some animals that produce altricial young, which are large enough to produce precocial young → This leads us to think that altriciality has some inherent value.

Production of immature young would have *freed the mother from retaining young inside of her* for an extended amount of time.

It might also be favored as a means of *increasing peak reproductive rate* → increased evolutionary fitness.

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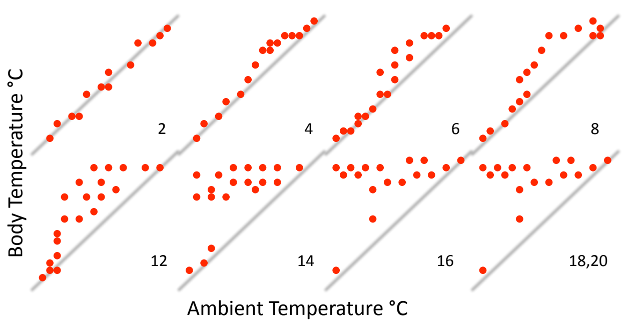
Endothermy: developmental aspects

Historical viewpoint (data from Hill, 1976)



These data were gathered on *Peromyscus leucopus* in isolated conditions. We see altriciality (i.e. delayed development) of endothermy in the above graphs.

These types of data have laid the ground work for theories of the evolution of thermoregulation. *But, there's a problem…*

Endothermy: developmental aspects

In reality, nestlings are hardly ever isolated: they are in an insulated nest, huddled with their littermates.

There is a significant amount of data showing that non-isolated altricial young do thermoregulate earlier than previous studies show:

• *P. leucopus* mothers can be absent from the nest 5-6 h/day

• To use energy for thermoregulation takes away from energy for growth, so it's a delicate balance.

Birds are slightly different than mammals: they appear to be completely devoid of thermoregulatory ability during most of their nestling life. However, they appear to grow faster than precocial ones.

Overall thermal balance

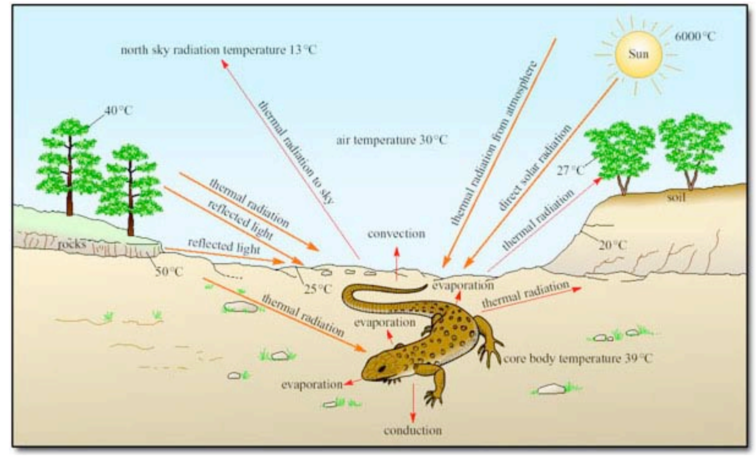
In the simplest form:

Body temperature = heat produced metabolically
+ heat gained from the environment
-Heat lost to the environment

Animals use four physical process to exchange heat with the environment: *conduction, convection, evaporation, and radiation*:

- *Conduction* is the direct transfer of heat between the animal and environment (e.g. sitting on the cold ground)
- *Convection* is the movement of a fluid over the surface of a body (e.g. wind or swimming)
- *Evaporation* is the loss of heat when water molecules escape in the form of gas
- *Radiation* is the emission of electromagnetic waves that objects, such as an animal's body or the sun, produce (e.g. an animal "sunning" itself)

Overall thermal balance

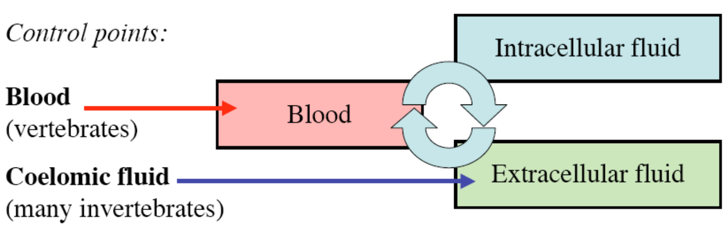


Water balance and osmoregulation

All animals must exchange materials and energy with their environments. External environments may be *very different* from the animal's ***internal*** environment, and may *change rapidly*; usually the internal environment needs to stay fairly constant.

Regulation of the animals internal composition within appropriate limits – a process called *homeostasis* – is largely done by monitoring and adjusting the composition of body fluids.

Body fluids can be thought of as a part of three fluid 'compartments':



Water balance and osmoregulation

Besides energy, gas exchange, nutrition, and heat balance, what are the major regulatory problems?

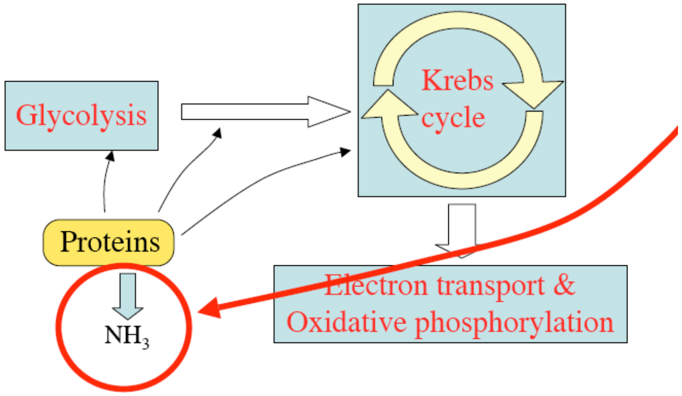
- **Nitrogen excretion**
- **Water balance**
- **Electrolyte (salt or ion) balance (solute balance)**

All of these processes are interrelated, all depend on the envinronment, and the way an animal handles one problem often influences the way it handles other problems.

Nitrogen metabolism and excretion

All animals metabolize proteins in cellular respiration (more in carnivores, less in herbivores)

'Burning' amino acids to make ATP (or converting them into other compounds) releases the amino group through **deamination**:



Nitrogen metabolism and excretion

Deamination releases ammonia (NH_3), the initial (primary) **nitrogenous waste**. This is toxic and must be disposed of.

- Some animals (**ammoniotelic**) excrete the ammonia directly
  - Biochemically simple and relatively cheap, but…
  - Ammonia is highly toxic, so it must be stored in low concentrations (i.e., ***lots* of water needed for disposal**)
  - Most common in aquatic species, which have plenty of water available
    - (freshwater bony fish, many invertebrates)

Nitrogen metabolism and excretion

The large amount of water loss needed for ammonia excretion is a problem for animals with limited access to water.

Solution: convert ammonia to less toxic nitrogen compounds; two are commonly used:

UREA (CN_2OH_4) and *URIC ACID* ($C_5N_4O_3H_4$)

UREA (ureotilic animals)

- highly soluble; fairly low toxicity: high concentrations OK
- excreting N as urea requires far less water than if ammonia were excreted
- urea excretion is energetically expensive: it costs substantiall amounts of ATP to convert ammonia to urea
- most important nitrogen excretion product in many land animals (mammals, adult amphibians); also used by some marine animals (marine mammals, sharks, sea turtles)

Nitrogen metabolism and excretion

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Solution: convert ammonia to less toxic nitrogen compounds; two are commonly used:

UREA (CN_2OH_4) and *URIC ACID* ($C_5N_4O_3H_4$)

URIC ACID (uricotilic animals)

- not very soluble; low toxicity; precipitates out of solutions and can be secreted as a semisolid paste
- Requires even less water than urea excretion
- Very energetically expensive (15 biochemical steps and considerable ATP)
- Most important nitrogen excretion product in birds, reptiles, insects (**shelled eggs** may have required a nontoxic, water-efficient N waste to protect embryo).

Osmoregulation: water and solute balance

Concentrations of major solutes (usually ions: Na^+, K^+, Cl^-, Ca^{2+}, hence called *electrolytes*) in the body need to be kept within reasonable limits, otherwise enzyme function, etc., is impaired.

- osmoconformers tend to be isoosmotic (or, isotonic) to the environment – osmolarity can be constant or variable (within limits), depending in environment.
- most animals are osmoregulators: they maintain an internal osmotic environment different from that in the environment
  - *Hyperosmotic:* higher osmotic potential than environment
  - *hypoosmotic:* lower osmotic potential than the environment

→ Must carefully balance solute uptake with solute removal

Osmoregulation: water and solute balance

Most animals (other than osmoconformers) have an internal osmolarity of roughly 300 milliosmoles/liter (roughly equal to a 0.9-1.0% saline solution)

Osmoregulatory problems for a terrestrial animal are:

- *loses water* by evaporation and in urine and feces
- *loses solutes* in urine and feces (and in some species, salt glands)

These losses need to be replaced at the same rates:

- *gains water* in food and (in some species) by drinking
- *gains solutes* in food (or by drinking, if water isn't fresh)

Some variation in water content is OK (depends on species):

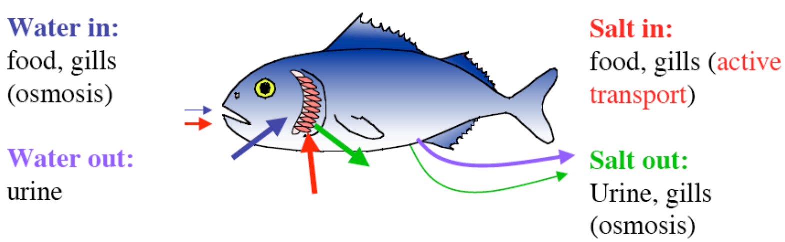
-- humans are in trouble if they lose more than ~10% of body water; camels are OK out to a loss of 20-25%

Osmoregulation: water and solute balance

What about aquatic animals? Skin impermeable, but gills are not.

Freshwater fish (300 mosm inside, 1-10 mosm outside)

- tends to ***gain*** water and ***lose*** salts



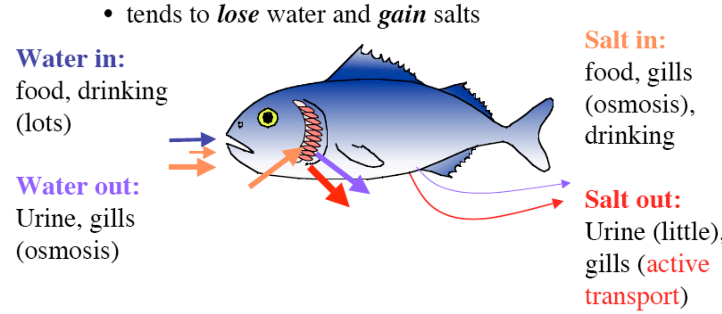
Active transport of solutes (here, salt gain in the gill) is *always* a factor in osmoregulation in hypo- or hyperosmotic environments: ***energy cost of osmoregulation.***

Osmoregulation: water and solute balance

What about aquatic animals? Skin impermeable, but gills are not.

Marine fish (300 mosm inside, 1000 mosm outside)

- tends to ***lose*** water and ***gain*** salts



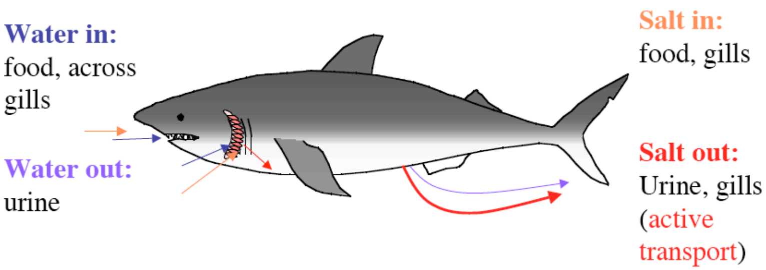
Active transport of solutes (here, salt loss in the gill) is *crucial*

Osmoregulation: water and solute balance

What about aquatic animals? Skin impermeable, but gills are not.

Sharks and rays: (1000 mosm outside): Body fluids of these fish contain ~ 300 mosm of 'normal' solutes…
plus lots of urea and trimethylamine oxide (TMAO)
total osmolarity ~ 1020 mosm (slightly ***hyperosmotic***)

- ***little*** net water flux; tend to gain salt



Osmoregulation: water and solute balance

What about marine reptiles, birds and mammals?

They **don't breathe through gills**, so aren't really exposed to sea water.

They do need to dispose of salt (especially if they drink sea water), and must do so in a form more concentrated than sea water (> 1,000 mOsm) or there will be a net water loss.

- marine mammals produce highly concentrated urine
- marine reptiles and birds have special **salt glands** (usually in the head) that produce a very salty solution (> 1,500 mOsm).

Humans cannot produce a urine more salty than sea water – so if we drink sea water, we **dehydrate**.

Excretory organs

Excretory organs in all multicellular animals work in basically a similar fashion:

- They **collect fluids** (either from blood or from extracellular fluids)
- They **modify the composition** of this excretory fluid:
  - Selective **reabsorption** of some substances
  - Selective **secretion** of waste products into the excretory fluid
  - **Active transport** important in both processes
- They provide a means for **expulsion** of the excretory fluid from the body.

In vertebrates the primary excretory organ is the **kidney**, and its functional units are small tubular structures called nephrons.

Excretory organs

Excretory organs in all multicellular animals work in basically a similar fashion:

- They **collect fluids** (either from blood or from extracellular

The primary challenge for mammalian kidneys:

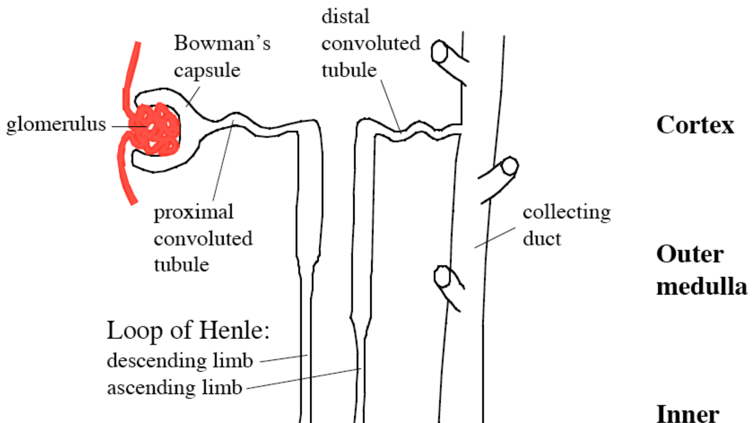
How to produce a hyperosmotic urine to minimize water loss in a dry terrestrial environment.

Both structure and function of the nephron are key.

- They provide a means for **expulsion** of the excretory fluid from the body.

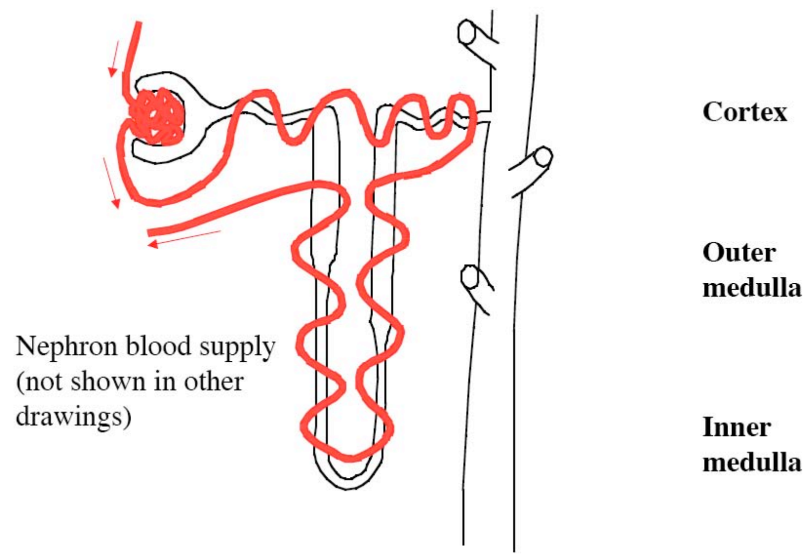
In vertebrates the primary excretory organ is the **kidney**, and its functional units are small tubular structures called nephrons.

Nephron structure and function

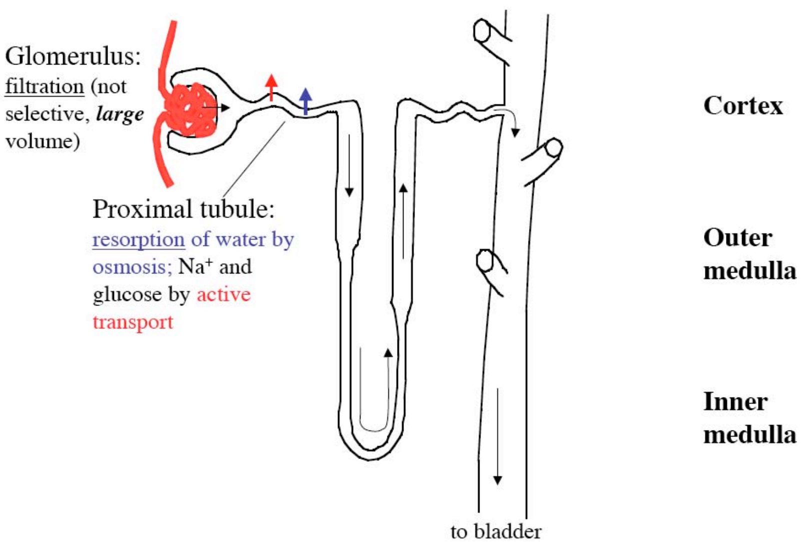


Not all nephrons have a large loop of Henle -- but many loops of Henle are always present in mammalian kidneys.

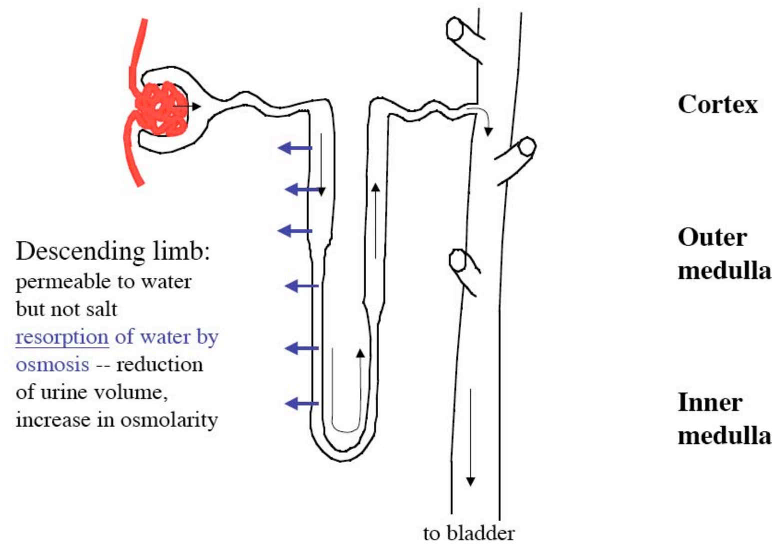
Nephron structure and function



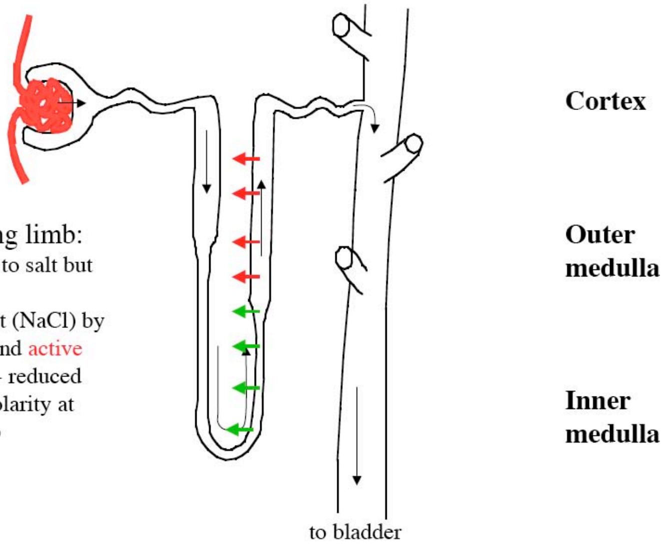
Nephron structure and function



Nephron structure and function

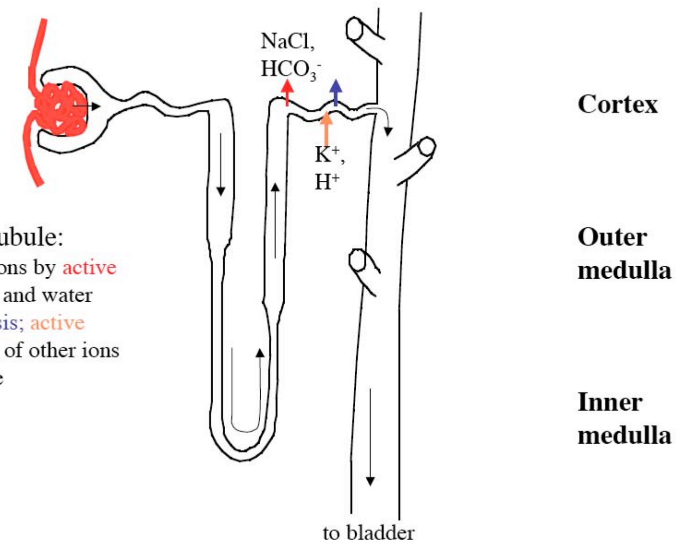


Nephron structure and function



Ascending limb:
permeable to salt but not water
Loss of salt (NaCl) by diffusion and active transport -- reduced urine osmolarity at top of loop

Nephron structure and function



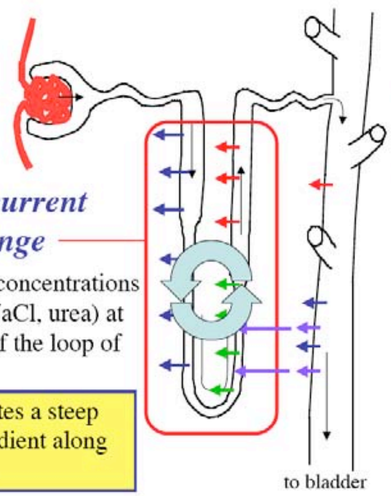
Distal tubule:
Loss of ions by active transport and water by osmosis; active secretion of other ions into urine

Nephron structure and function

Countercurrent exchange

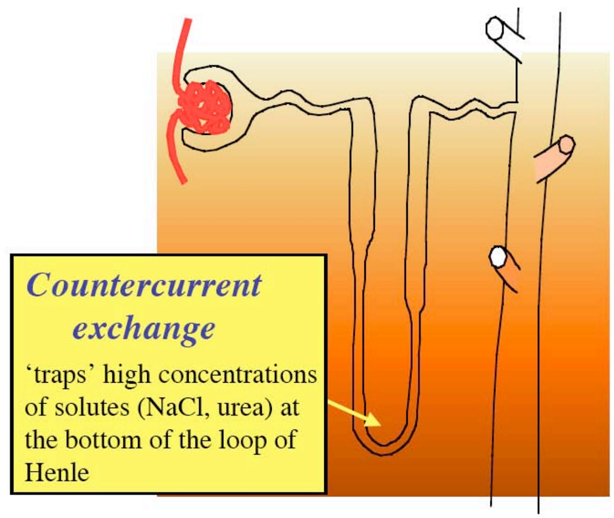
'traps' high concentrations of solutes (NaCl, urea) at the bottom of the loop of Henle.

This generates a steep osmotic gradient along the loop…



Collecting duct:
Loss of NaCl by active transport and water by osmosis; loss of urea by diffusion (some uptake in ascending limb)

Nephron structure and function



about 100-200 mosm
hypoosmotic to blood

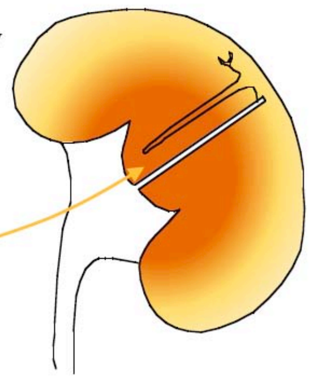
This generates a steep osmotic gradient along the loop…

about 1200 mosm

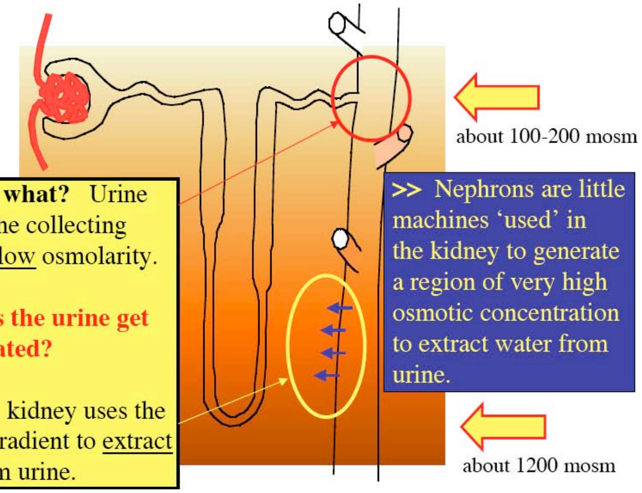
Nephron structure and function

… and in the kidney as a whole:

Thousands of nephrons are lined up in the same orientation; interior (medulla) of kidney is a region of high solute concentration.



Nephron structure and function



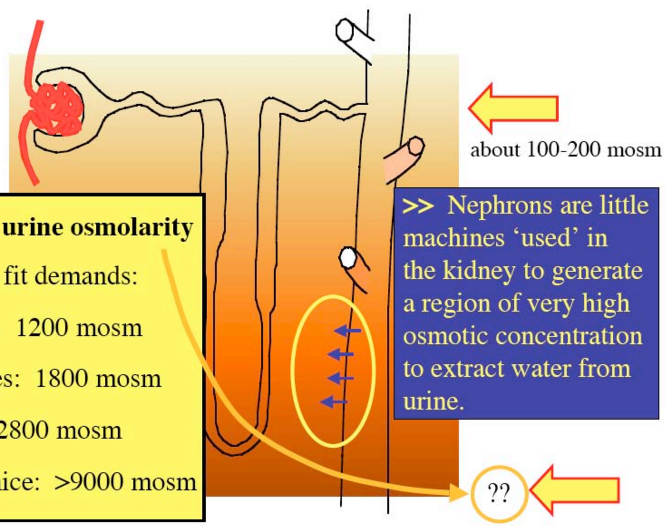
… but so what? Urine entering the collecting duct is at low osmolarity.

How does the urine get concentrated?

kidney uses the osmotic gradient to extract water from urine.

>> Nephrons are little machines 'used' in the kidney to generate a region of very high osmotic concentration to extract water from urine.

Nephron structure and function

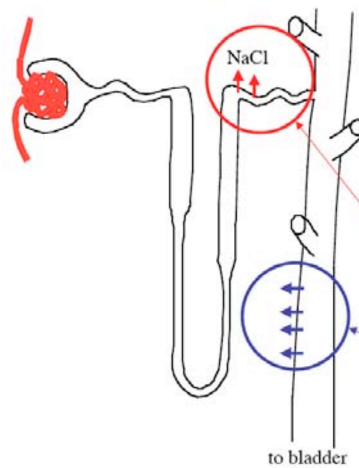


Maximum urine osmolarity evolves to fit demands:

- humans: 1200 mosm
- porpoises: 1800 mosm
- camel: 2800 mosm
- desert mice: >9000 mosm

>> Nephrons are little machines 'used' in the kidney to generate a region of very high osmotic concentration to extract water from urine.

Control of urine volume and osmolarity

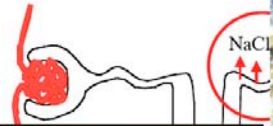


Animals must adjust urine volume and composition, from large volumes of dilute urine to small volumes of concentrated urine.

Control points:

- Adjust NaCl resorption in distal tubule (**aldosterone**, other hormones)
- Adjust permeability of collecting duct to water (**vasopressin: anti-diuretic hormone; ADH**)

Control of urine volume and osmolarity



Vampire bat:

- eats lots of blood; while eating, voids lots of dilute urine (saves weight)
- in roost, high-protein meal produces lots of **urea**; no water available so bat produces small volumes of very concentrated urine (4500 mosm)