Osmoregulation, ion regulation, nitrogen waste excretion
Animal Cells have osmotic issues...
Review Diffusion -

The molecules are solutes.

If this is an aqueous solution, water is the solvent.
OSMOSIS

Water moves from areas of higher concentration to areas of lower concentration.

1. Start with more solute on one side of the selectively permeable membrane than the other, using molecules that cannot cross the membrane.

2. Water moves from the region of lower concentration of solutes (higher concentration of water) to the region of higher concentration of solutes (lower concentration of water).
cell membranes can't hold back osmotic pressure (but plant cell walls can)

must accommodate water. Force balances when solute density same on both sides = no osmotic pressure
Ocean: about 500 mM Na⁺, 500 mM Cl⁻
1000 mOsm

Animal cell in ocean

Must be iso-osmolar with surroundings

1000 mOsm inside
1000 mOsm outside
No problem...

Otherwise it will shrink or swell

EXCEPT...
Cell needs proteins, nucleic acids, etc inside -- must have stuff to be alive!!

So ... to be iso-osmolar, concentration of Na\(^+\), Cl\(^-\) inside must be less than outside

\[ \text{Na}^+ \text{Cl}^- \rightarrow \text{want to flow in, down their concentration gradients} \]

\[ \Rightarrow \text{cell must expend energy to pump out salt} \]
Rather than make each cell do the work, animals build an organ system to maintain correct internal ionic-osmo-concentration.

Add a skin barrier so the inside is not equal to the outside.

The mechanism needed, and how it works, depends on the environment in which you evolved:

1. Marine non-bony fish (Elasmobranchs)
2. Fresh water bony fish
3. Marine bony fish
4. Terrestrial organisms - first insects, then vertebrates

Once animals invade land, osmoregulation becomes entwined with excretion of nitrogen waste.
Terminology swamp... for the purposes of this course:

Isotonic = iso-osmotic
         or
         iso-ionic
         or
muscle contraction with no movement.

Hypertonic, hypotonic = unequal salt or unequal osmotic.

Iso-osmotic = same osmotic concentration
Sharks: A non-bony (non-teleost) marine vertebrate.

Sharks evolve in oceans less salty than today.

Present oceans more salty than shark’s tissues.

Shark has problem with ion gain (= water loss)
Salt flows in at gills down its concentration gradient. So...

Use ion Pump to dump excess salt.
How does the shark make an ion pump??
4 separate transport pumps... but how does it really work?
In each cell of the salt excretion organ –

The channels or transporters or pores are composed of membrane-spanning proteins.

Cells are clever, and can insert the channels in just certain regions of their membrane (say one side or the opposite side), and with a particular orientation.
multi-domain membrane spanning protein -> assembles to form a pore (= channel).

Can be selective for certain ions, can allow co-transport (symporter), or have ATPase power.
All of the parts… but let’s go one step at a time (next slides)
1. Pump Na\(^+\) OUT of the cell back into the fish! Wrong direction!! (will fix later).
2. An open channel on inside side of cell membrane allows K\(^+\) to leak back out.
Use steeeeep Na\(^+\) gradient to power a Cl\(^-\) and K\(^+\) pump. (= “co-transport”)

---

STEP 2

Na\(^+\) cycles too

Na\(^+\) pumped out

Na\(^+\) gradient

HUGE

Nat. from blood

powers co-transport

\(\delta\) Cl\(^-\) & K\(^+\)
A Cl⁻ channel just on the outside face of the cell allows Cl⁻ ions to flow down their gradient out of the shark.

STEP 3

So Na⁺-K ATPase + co-transporter net effect is to move chloride!!

↓

charge gradient across cell

net because Na⁺, K⁺ cycle
The Cl\textsuperscript{-} concentration outside creates an electrostatic force field pulling Na\textsuperscript{+} to the outside (unlike charges attract!).

This leads to a net loss of Na\textsuperscript{+} and Cl\textsuperscript{-}, which is the goal of the rectal gland.
MODEL OF SALT EXCRETION IN SHARK RECTAL GLAND

Lumen side (interior of gland empties into environment)

Apical membrane

Epithelial cells of rectal gland

Basolateral membrane

ATP
ADP
Na⁺/K⁺-ATPase

3Na⁺

Cl⁻
Chloride channel

Na⁺

2K⁺

Na⁺/K⁺-cotransporter

2Cl⁻

K⁺

Potassium channel

Extracellular fluid, near blood vessels

1. Na⁺/K⁺-ATPase pumps Na⁺ out of cell and K⁺ into cell, creating an electrochemical gradient favoring diffusion of Na⁺ into cell and K⁺ out.

2. Na⁺/Cl⁻/K⁺ cotransporter, powered by the gradient favoring Na⁺ diffusion, brings these three ions from the extracellular fluid into epithelial cells across their basolateral surfaces.

3. K⁺ diffuses out through channels in basolateral membrane. Cl⁻ diffuses into lumen along its concentration and charge gradients.

4. Na⁺ diffuses into lumen along its concentration and charge gradients.

Figure 42-5 Biological Science, 2/e
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Cartilaginous fishes evolve in marine environment.

Ancestral species invade fresh water streams.

So all marine bony fish had fresh water ancestors, and thus use different methods for ion & osmo regulation re: non-bony marine fishes.

Marine teleost fishes evolve.

Ancestral species re-invade marine environment.

Teleost (bony) fishes evolve in fresh water.

... and now for a bit of fish evolution
Marine fish evolved in oceans where the salinity was $1/4 - 1/3$ of the present amount.

All vertebrates still have blood ionic concentrations that are $1/4$ to $1/3$ of the current ocean salinity, but equal to the ancient salinity level.

So...

Marine teleost fish tissues are hypo-ionic relative to seawater.

Fresh water teleost fish tissues are hyper-ionic relative to fresh water.
The first vertebrates to leave salt water: fresh water fish

**Freshwater**

- Gain some electrolytes in food
- Lose electrolytes through gills by diffusion
- Gain water through gills by osmosis
- Lose some electrolytes in urine
- Lose water in urine formation

How to dump excess water entering at gills?
How to recapture salt leaving at gills?
2 tricks to dump excess water and suck up as much salt as possible from the environment:

1. Gill chloride cells.

2. The glomerular kidney.
1. gill chloride cell (in fresh water fish)

1. chloride-bicarbonate ion co-exchanger
2. sodium-proton exchanger
3. sodium-potassium pump

Note: Actually 2 cells needed – one has Cl⁻ pump and the other has Na⁺ pump)
1. $\text{Cl}^-$ pumped in from outside, then diffuses into the fish.

2. Sodium pumped in from outside, then pumped into the fish.
2. Glomerular Kidney

The Glomerulus/Bowman’s capsule allows separation of blood.
Divide blood into (a) mostly water and salts and (b) cells, proteins.

Then recover salt, and dump excess water.
Mostly water and salt channel = "filtrate".

Sludgy blood and protein in vein leaving capsule.
Next step — recover water, salt

Filtrate from capsule

kidney tubule

"Brush-border" cells line tubule

renal vein blood

Salt transport
Sodium-potassium ATPase pump

\[ \text{Na}^+ \text{ out of cell at serosal side} \]

"Mucosal" side

(lumen of tubule)

\[ \text{K}^+ \]

\[ \text{H}_2\text{O} \]

\[ \text{Na}^+ \]

\[ \text{K}^+ \]

\[ \text{H}_2\text{O} \]

\[ \text{Na}^+ \text{ gradient made by pumping} \]

\[ \text{K}^+ \text{ follows} \]

\[ \text{WATER follows osmotically} !! \]
Filtrate will be excreted

B.B. cell

Salt

H₂O

B.B. cell

↑ Tight junctions between B.B. cells prevent leaks!

Along proximal kidney tubule
70% of salt & water recovered.

Water, salt back into circulation
How does this help the fresh water fish?

Ans: The 30% of water that is **not** recovered!
Filtrate will be excreted

β.B. cell

Salt

H₂O

Tight junctions between β.B. cells prevent leaks!

Renal vein blood

β.B. cell

H₂O

Osmosis

Na⁺ Cl⁻ Osmosis

Na⁺ Vitamins

Cl⁻

Glucose

Na⁺

2K⁺

ATP

ADP

3Na⁺

1

2

3

4

Glucose H₂O Osmosis

Cl⁻ Vitamins
Marine environment is saltier than fish's tissues:

Water flows down its gradient OUT of the fish.

To compensate, marine fish drink lots of seawater, then pump out excess ions using chloride cells in gills.

What happens when teleosts, having evolved in fresh water, invade the ocean (& revisit their elasmobranch ancestors)
Marine teleost fish: Gill chloride cells reverse direction (re: fresh water fish) and pump salt out.

1. Na⁺ powered Cl⁻, K⁺ xport
2. Na⁺-K⁺ pump
3. Na⁺ diffusion
The **last** thing marine teleost fish want to do is dump water, but they have inherited the fresh water glomerulus!

Marine teleost fish cut blood flow to kidneys \( \rightarrow \) much less blood flow to glomeruli, so much less filtrate produced:

Fresh water teleost: \( 3 \text{ ml kg}^{-1} \text{ hr}^{-1} \) filtrate secreted, \( 20 \text{ mOsm} \)

Salt water teleost: \( 0.3 \text{ ml kg}^{-1} \text{ hr}^{-1} \) filtrate secreted, \( 410 \text{ mOsm} \)

\( 1/10^{\text{th}} \) as much!
More osmoregulation terms:

**Euryhaline** – can tolerate wide range of osmolarity

**Stenohaline** – can tolerate only a narrow range of osmolarity

A hyper-ionic environment is hyper-tonic to the animal.

A hyper-osmotic environment is hyper-tonic to the animal.

A hyper-tonic environment causes the animal to shrink by water loss.
Salmon – the “polarity” of the chloride cells in the gills changes when the fish migrate from fresh → salt water → fresh water.

That is, the transport proteins move from the basolateral cell surface to the apical cell surface, so ions are pumped in or out of the fish, depending on the osmotic/ionic environment.
Migration to the ocean and back

Freshwater breeding ground (hypotonic environment)

Young salmon migrate downstream.

Sexually mature adults return to freshwater to breed.

Most salmon spend 3–5 years in the open ocean, feeding and growing.

Ocean (hypertonic environment)

Hmm... hypertonic?
Salmon in freshwater

Chloride cells located on lamellae of gill filaments import electrolytes

Salmon in seawater

Chloride cells located at base of gill filaments secrete electrolytes
Kidneys are the principle iono- osmo- regulation organ…

BUT

They have an equally important role in getting rid of nitrogen waste.
Protein metabolism creates ammonia

Fish, aquatic invertebrates dump ammonia to the environment via gills.

→ Infinite dilution factor!

Ammonia!! (really toxic)
Terrestrial environment: big problems for ion/osmo regulation and nitrogen waste excretion.

1. Must keep from drying out (ion conc. problem)!

2. Must dump ammonia without losing much water!

So aquatic orgs – no problem with ammonia.

*What happens when terrestrial orgs evolve?*
The first animals to invade land are insects.

1a. Oxygen ventilation system reduces water loss from respiratory epithelia.

Spiracles can be closed to minimize water loss from tracheae.

Figure 42-9a Biological Science, 2/e © 2005 Pearson Prentice Hall, Inc.
This is a better deal than humans – we use evaporative cooling (= water loss!!) to maintain Tb.

Humans at 100 °F: Water loss is one liter per hour!!
TRICK TO DEAL WITH AMMONIA —

turn it into something non-toxic.

2 inventions

⇒ urea: OK if can afford some water loss

⇒ uric acid: best if really need to minimize water loss

UREA

\[ \begin{array}{c}
\text{O} = \text{C} \\
\text{N} \text{H}_{2} \\
\end{array} \]

non-toxic (+/-)
water soluble
can store in body tissues

URIC ACID

\[ \begin{array}{c}
\text{O} = \text{C} \\
\text{N} \text{H} \\
\end{array} \]

⇒ EXPENSIVE
Table 42.1  Attributes of Nitrogenous Wastes Produced by Animals

<table>
<thead>
<tr>
<th>Attribute</th>
<th>Ammonia</th>
<th>Urea</th>
<th>Uric Acid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Solubility in water</td>
<td>high</td>
<td>medium</td>
<td>very low</td>
</tr>
<tr>
<td>Water loss (amount required for excretion of waste)</td>
<td>high</td>
<td>medium</td>
<td>very low</td>
</tr>
<tr>
<td>Energy cost (amount of ATP required)</td>
<td>low</td>
<td>high</td>
<td>high</td>
</tr>
<tr>
<td>Toxicity</td>
<td>high</td>
<td>low</td>
<td>medium</td>
</tr>
<tr>
<td>Groups where it is the primary waste</td>
<td>fish</td>
<td>mammals(^*)</td>
<td>birds(^†), reptiles</td>
</tr>
<tr>
<td></td>
<td>aquatic invertebrates</td>
<td>sharks</td>
<td>most terrestrial insects</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>and spiders</td>
</tr>
<tr>
<td>Method of synthesis</td>
<td>breakdown of amino acids and nucleic acids</td>
<td>synthesized in liver, starting with amino groups from amino acids</td>
<td>synthesis starts with amino acids and nucleic acids</td>
</tr>
<tr>
<td>Method of excretion</td>
<td>in urine and diffuses across gills</td>
<td>in urine (mammals); diffuses across gills (sharks)</td>
<td>in feces (in birds, uric acid is derived from the urine but excreted with the feces)</td>
</tr>
</tbody>
</table>

\(^*\)Mammals also excrete a small amount of uric acid, synthesized from excess nucleic acids.

\(^†\)Birds also excrete a small amount of ammonia.

Note use of term “primary” waste. Most mammals make all three waste products, but the ratio is highly skewed to one or another.
So now the challenge is to get rid of the urea or uric acid and NOT get rid of other components of extra-cellular (hemocoel/plasma) fluids or water.

The trick will be to use osmotic gradients and selective permeability ion channels to build an “osmotic concentrator”.
Insects excrete hypertonic (to body fluids) waste stream. So little $\text{H}_2\text{O}$ leaves that a dry uric acid precipitate is left.

**Diagram:**
- **Midgut:**
  - Flow
  - Active transport
    - Uric acid
    - $\text{Na}^+, \text{K}^+$
    - $\text{H}_2\text{O}$

- **Hindgut:**
  - Uric acid stays!
  - $\text{Na}^+, \text{K}^+$
  - $\text{H}_2\text{O}$

  - Active transport
  - Via osmotic drag
    - Malphigian tubule

- **Rectum:**
  - Osmotic drag
  - And precipitates!
Malpighian tubules produce an isotonic pre-urine.

Uric acid dumped
Under osmotic stress, the hindgut reabsorbs electrolytes and water to form a hypertonic urine.
Bug poop – dry, very little water loss.
What happens when *vertebrates* invade land?

Amphibians evolve from fresh water fish, and have essentially the same kidney as fish… so they make lots of dilute urine as a way to dump excess water…

*except!!!!*

As with marine fish, this is the last thing a terrestrial organism wants to do.

Amphibians invent a solution – a big bladder. Dump the water, but save it. Frogs and toads can retrieve water from their bladders!

*(BTW, amphibian skin does NOT represent a barrier to water loss)*
The “more-terrestrial” vertebrates – reptiles & birds - come up with yet more adaptations:

- Keratinized (water impermeable) skin
- Specialized salt pumping (more coming up on this)
- Uric acid production (convergence with insects)
- The long loop of Henle
Terrestrial vertebrate salt pumping:

We can just re-invent the shark rectal gland to make a “salt gland”.

Terrestrial birds and reptiles that get extra salt in their diet use salt pumping to get rid of this excess.

For example, birds that fish in the ocean and marine iguanas.
Where you find salt glands in reptiles?

**Marine Iguana** – nasal gland, sneezes

**Snakes, Turtles** - supraorbital gland, drain secretions into the orbit (turtles) or oral cavity (snakes)

**Crocodiles** – sublingual salt glands, drain into oral cavity
Structure of Bird Salt Gland

- Skull
- Eye
- Nasal cavity
- Artery
- Vein
- Central canal
- Secretory tubule
- Capillaries
- NaCl
The salt gland uses a counter-current exchanger:
A counter-current exchanger in the salt gland

Flow in the gland lumen is opposite the blood flow
Where does the salt go?

Salt crystals encrusting nose of lizard
Amount of salt concentration in salt glands

Note hyper-ionic concentration over sea water. Herring gulls can transport salt via salt glands at 20x the rate (per gram of tissue) as a human kidney!

Concentration of sodium in the nasal secretion of different species of birds. The chloride concentration in a given sample is nearly identical to the sodium concentration, and other ions are found only in small amounts. [Schmidt-Nielsen 1960]

<table>
<thead>
<tr>
<th>Species</th>
<th>Sodium concentration (mmol liter$^{-1}$)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Duck, mallard</td>
<td>400–600</td>
</tr>
<tr>
<td>Cormorant</td>
<td>500–600</td>
</tr>
<tr>
<td>Skimmer, black</td>
<td>550–700</td>
</tr>
<tr>
<td>Pelican, brown</td>
<td>600–750</td>
</tr>
<tr>
<td>Gull, herring</td>
<td>600–800</td>
</tr>
<tr>
<td>Gull, black-backed</td>
<td>700–900</td>
</tr>
<tr>
<td>Penguin, Humboldt’s</td>
<td>725–850</td>
</tr>
<tr>
<td>Guillemot</td>
<td>750–850</td>
</tr>
<tr>
<td>Albatross, blackfooted</td>
<td>800–900</td>
</tr>
<tr>
<td>Petrel, Leach’s</td>
<td>900–1100</td>
</tr>
</tbody>
</table>

---

Concentration of sodium and potassium (mmol per liter) in sea water and in salt gland secretion. (From Schmidt-Nielsen, 1990)

<table>
<thead>
<tr>
<th>Species</th>
<th>Na$^+$</th>
<th>K$^+$</th>
<th>Ratio: Na$^+$/K$^+$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sea water</td>
<td>470</td>
<td>10</td>
<td>47</td>
</tr>
<tr>
<td>Sea turtle (Lepidochelys)$^b$</td>
<td>713</td>
<td>29</td>
<td>25</td>
</tr>
<tr>
<td>Sea snake (Pelamis)$^b$</td>
<td>607</td>
<td>28</td>
<td>24</td>
</tr>
<tr>
<td>Estuarine crocodile (Crocodylus)$^c$</td>
<td>663</td>
<td>21</td>
<td>32</td>
</tr>
<tr>
<td>Marine iguana (Amblyrhynchus)$^b$</td>
<td>1434</td>
<td>235</td>
<td>6.7</td>
</tr>
<tr>
<td>False iguana (Ctenosaura)$^d$</td>
<td>78</td>
<td>527</td>
<td>0.15</td>
</tr>
<tr>
<td>Chuckawalla (Sauromalus)$^d$</td>
<td>121</td>
<td>379</td>
<td>0.32</td>
</tr>
</tbody>
</table>

Mammals use a different trick for salt concentration:

Add a long loop of Henle to (many) kidney tubules.

Next – let’s look at the general structure of mammalian kidneys →
This allows mammals (and only mammals) to make urine more concentrated than their blood plasma.

In some nephrons, the loop of Henle is long and plunges into the medulla.

In most nephrons, the loop of Henle is relatively short and is located in the cortex.
Many nephrons working in parallel

(Loops of Henle not shown)
Blood supply

(a) Nephrons have five major regions.

1. Renal corpuscle
2. Proximal tubule
3. Loop of Henle
4. Distal tubule
5. Collecting duct

(b) Blood vessels serve each nephron.

- Blood enters
- Blood leaves

Water and solutes from the loop of Henle move into blood vessels (vasa recta)

Final urine to ureter

Figure 42-12 Biological Science, 2/e
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Figure 42-17 Biological Science, 2/e
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Mammalian kidney retains Bowman’s capsule – still very effective for recapturing water:

Mammals: Very high pressure system → huge amounts of filtrate.

Blood flow in the renal artery is 125 mls per minute.

Humans kidney -- 1% of body mass but receives 25% of cardiac output!!

Of the 125 mls/min, 70% is recovered in the proximal tubule (like the fresh water fish!).

Loop of Henle → recover the remaining 30% (+/-).
How the loop works
Three essential parts:

1. Descending loop
2. Ascending loop
3. Salt gradient.
Basic idea: build an osmotic concentration gradient in interstitial fluid — use gradient to drag back water.
salt, water, urea

Capture salt, water

Salt, water, urea

Salt, water

Salt, water

Salt, water

Salt, water

Salt pumped out

Salt

Urea

Urea

Urea

Concentrate urea

Blood
Mind these numbers!

Descending limb is highly permeable to water but impermeable to solutes

Ascending limb is impermeable to water but highly permeable to $\text{Na}^+$ and $\text{Cl}^-$

Figure 42-16b Biological Science, 2/e
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Three separate mechanisms control water retention/release by the kidney:

1. **Anti-diuretic hormone**: acts on collecting duct (osmotic pressure). Antidiuretic hormone = ADH = arginine vasopressin)

2. **Aldosterone**: acts on distal tubule (anti-hypotension)

3. **Renin-angiotensin**: acts on circulatory system, brain, and more (anti-hypotension)
Collecting Duct:

• Differentially reabsorbs water and solutes.

• Controlled by modulating the permeability of the walls of the tubule to water.

  - High permeability $\rightarrow$ water leaves collecting duct $\rightarrow$ concentrated urine
  
  - Low permeability $\rightarrow$ water stays in collecting duct $\rightarrow$ dilute urine
Apical cells of collecting duct have receptors for ADH molecules.

Bind ADH $\rightarrow$ intracellular signal generated $\rightarrow$ transcription regulation $\rightarrow$ make more aquaporin molecules (AQP-2).

AQP-2 inserted into apical cell membranes $\rightarrow$ more water flow out (back into animal).
ADH present: Collecting duct is highly permeable to water.
No ADH present: Collecting duct is not permeable to water.
If blood osmotic pressure is high / blood pressure low:

Detected by osmosensor cells in hypothalamus $\rightarrow$ posterior pituitary secretes large amounts of ADH

$\rightarrow$ Aquaporin-2 molecules inserted into the collecting duct $\rightarrow$
  - increase permeability of the collecting duct
  - water retained in blood

$\rightarrow$ blood osmotic pressure reduced, blood pressure increases
2. Aldosterone: defends blood pressure

- Released from adrenal cortex

- Regulates Na\(^+\) uptake (Apical Channels in distal tubule) by increasing the transcription of Na\(^+\) pumps.

- An increase in Aldosterone increases blood pressure.
Aldosterone → more Na+ pumps → more water retained

Osmotic drag of water
3. Renin-Angiotensin: Defends blood pressure

• Renin release from kidney by…
  o Sympathetic stimulation
  o renal artery hypotension (baro-receptors)
  o decreased sodium delivery to the distal tubules

• Renin is an enzyme, cleaves the circulating substrate angiotensin I (A-1).

• Angiotensin converting enzyme (ACE) in lungs (!!) cleaves two amino acids from A-1 → octapeptide angiotensin II (A-II).
Too little blood pressure: JGA $\rightarrow$ renin release.

Angiotensinogen $\downarrow$ renin

Angiotensin I $\downarrow$ ACE

Angiotensin II $\downarrow$ aldosterone

Adrenal cortex

Retain salt, water

Blood volume

Blood pressure

Juxtaglomerular Apparatus (JGA) is a pressure sensor.

Angiotensinogen, a liver made globulin.
Sympathetic Stimulation
Hypotension
Decreased Sodium Delivery

Kidney \rightarrow Renin \rightarrow Angiotensinogen

Renin \rightarrow AI \rightarrow ACE

AI \rightarrow Adrenal Cortex

AII \rightarrow Pituitary

Thirst

AII \rightarrow Cardiac & Vascular Hypertrophy

AII \rightarrow Systemic Vasoconstriction

Increased Blood Volume

AII \rightarrow Renal Sodium & Fluid Retention

AII \rightarrow Aldosterone

Multiple functions of angiotensin II
Super kidneys
The longer the loop, the steeper the gradient that can be formed!
## Desert & Marine Mammals

Note very high urine concentration in some mammals

### Comparison of urine osmolality and urine-to-plasma ratios as indices of concentrating ability among various terrestrial and marine mammals (From Ortiz, 2001)

<table>
<thead>
<tr>
<th></th>
<th>Urine osmolality (mosmoll^{-1})</th>
<th>Urine: plasma ratio</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Terrestrial</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Human</td>
<td>1400</td>
<td>4.6</td>
<td>Vander, 1995</td>
</tr>
<tr>
<td>Dog</td>
<td>1800</td>
<td>6</td>
<td>DiBartola et al., 1980</td>
</tr>
<tr>
<td>Camel</td>
<td>2800</td>
<td>7</td>
<td>Ben Goumi et al., 1993</td>
</tr>
<tr>
<td>Domestic cat</td>
<td>3100</td>
<td>10</td>
<td>Schmidt-Nielsen, 1990</td>
</tr>
<tr>
<td>Kangaroo rat</td>
<td>5500</td>
<td>14</td>
<td>Schmidt-Nielsen, 1990</td>
</tr>
<tr>
<td>Hopping mouse</td>
<td>9400</td>
<td>25</td>
<td>Schmidt-Nielsen, 1990</td>
</tr>
<tr>
<td><strong>Marine/aquatic</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>West Indian manatee</td>
<td>1158</td>
<td>3.7</td>
<td>Irvine et al., 1980; Ortiz et al., 1998</td>
</tr>
<tr>
<td>Sei whale</td>
<td>1353</td>
<td>3.8</td>
<td>Fetcher, 1939</td>
</tr>
<tr>
<td>American river otter</td>
<td>1482</td>
<td>4.8</td>
<td>Hoover and Tyler, 1986</td>
</tr>
<tr>
<td>Rough-toothed dolphin</td>
<td>1700</td>
<td>5.0</td>
<td>Malvin and Rayner, 1968</td>
</tr>
<tr>
<td>Bottlenose dolphin</td>
<td>1815</td>
<td>5.3</td>
<td>Malvin and Rayner, 1968</td>
</tr>
<tr>
<td>Weddell seal</td>
<td>1760</td>
<td>5.6</td>
<td>Kooyman and Drabek, 1968</td>
</tr>
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<td>Northern elephant seal</td>
<td>1850</td>
<td>5.9</td>
<td>Ortiz et al., 1996</td>
</tr>
<tr>
<td>Grey seal</td>
<td>2161</td>
<td>6.0</td>
<td>Skog and Folkow, 1994</td>
</tr>
<tr>
<td>Harbor seal</td>
<td>2050</td>
<td>6.2</td>
<td>Page et al., 1954; Tarasoff and Toews, 1972</td>
</tr>
<tr>
<td>Sea otter</td>
<td>2130</td>
<td>6.7</td>
<td>Costa, 1982</td>
</tr>
<tr>
<td>Ringed seal</td>
<td>2420</td>
<td>6.8</td>
<td>Portier, 1910</td>
</tr>
<tr>
<td>Baikal seal</td>
<td>2374</td>
<td>6.9</td>
<td>Hong et al., 1982</td>
</tr>
<tr>
<td>Cape fur seal</td>
<td>2364</td>
<td>7.0</td>
<td>Bester, 1975</td>
</tr>
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</table>

Data for marine mammals were used only if plasma osmolality was also available in the same or another reference. The West Indian manatee, American river otter and Baikal seal are freshwater species.

Of course you don’t have to memorize these numbers!
Dolphin salt excretion rate (just FYI)

Excretion of solutes by the dolphin after feeding. A female *T. truncatus* (101 kg) was fed 4.7 kg of mackerel and 2 h later given 1 L SW by stomach tube (shown as hour 0). The first urine sample was taken 1 h after the SW, but the urine was forming throughout this period and analytical values are placed midway between 0 and 1 h. The urine was collected periodically and assayed for volume (○—○), osmolality (x—x) and urea (●—●) concentration. Values were also obtained for Na\(^+\) and Cl\(^-\) (not shown). The lower dashed line represents mean urine volume of a fasted animal, and the upper dashed line is the average osmolarity during fasting. [Drawn from data in Ridgway (231).]
When things go bad

Two common problems:

• Diabetic nephropathy: damage to the nephrons from unused glucose in the blood

• High blood pressure: can damage the small blood vessels
Uncontrolled diabetes: Need to urinate all the time.

Why?

**Normal:** Glucose in blood → ends up in filtrate. All glucose is transported back to blood.

**Diabetic:** Huge amounts of glucose in blood. Saturate transporters in proximal tubule, **not all** glucose transported back to blood.

- **Urine has high osmotic pressure.**
- **Less water dragged out by salt gradient.**
- **More water to bladder.**
Still lots of glucose in blood.

= Increase in blood osmotic pressure.

Osmosensors in hypothalamus: Must be dehydrated!

Bladder fills up even faster.

Drink more water

To brain: Dry mouth sensation, thirst sensation