CHAPTER 2

WATER RELATIONS

Water is naturally essential for life but the efficiency with which animals use water varies remarkably. Witness the almost effortless osmoregulation of a gull drinking sea water and the agonising thirst of the shipwrecked human. This chapter will explore this variability and has a similar structure to the preceding chapter in that we shall first discuss the physical aspects, then certain fundamental mechanisms involved in the physiological control of water balance in animals, before moving to actual case studies.

2.1 Physical properties of water

In nearly every introductory biology text, students are informed that water has ideal physical properties for supporting life. This approach is philosophically incorrect because water was present on this planet long before life arose and it would be far more correct to explain that life processes, as we know them today, have evolved largely around the very peculiar properties of water. Edney (1977) has written a useful and lucid review of the importance of these physical properties and this brief description depends heavily on his account.

The molecular structure of water (Fig. 2.1), as one would expect, determines its physical properties (Table 2.1). Stronger intermolecular forces are the reason for its higher melting and boiling points compared with substances with a similar structure. These intermolecular forces are the result of attraction between the two hydrogen atoms of one water molecule and the oxygen atoms of two adjacent molecules. This hydrogen bonding constitutes an energy store of 20 kJ mol^{-1}. When water is frozen, almost all the water molecules are hydrogen bonded. If the ice melts approximately 15% of these bonds are broken and the breaking of the bonds during melting requires the heat of fusion of ice (6 kJ mol^{-1} of water). The remaining hydrogen bonds must be broken before evaporation of water into vapour occurs and the energy required for this process is much greater (44 kJ mol^{-1} at 25 °C and 40 kJ mol^{-1} at 100 °C).

As we all know, water bounces readily off a solid surface but it is difficult to compress. For the latter reason it can be employed in hydraulic systems such

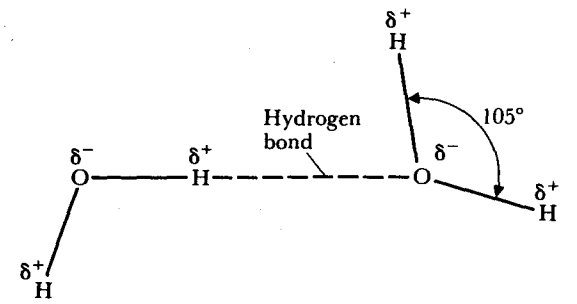


Figure 2.1 Structure of water molecules, showing the hydrogen bonding between hydrogen δ^+) in one molecule and on an oxygen (δ^-) in a neighbouring molecule.

Table 2.1 A comparison of the physical properties of water

Liquid	Heat of vaporisation (cal g $mole^{-1}$)	Melting point (°C)	Boiling point (°C)	Thermal capacity (cal g^{-1} K^{-1})	Dielectric constant
Water (HOH)	10 440	0	100	1.000	80.10
Hexane (C_6H_{14})	7 627	−95	49	0.535	1.89
Ethanol (C_2H_5OH)	9 673	−114	79	0.587	24.30
Mercury (Hg)	17 447	−38	357	0.033	—

as the flexible hydrostatic skeletons in many aquatic invertebrates. The flexibility of the skeleton and the poor compressibility of water are exploited in many invertebrate species to provide an appropriate mechanism for locomotion. The high heat of vaporisation of water, and its thermal capacity, are of crucial importance in the evaporative cooling of animals and the distribution of heat in aquatic habitats. The water molecule is polar and water is generally well suited to act as a solvent for the variety of biochemicals and electrolytes which have become incorporated in living organisms during evolution.

Water is not only an important solvent in the tissues of plants and animals, but it also takes part in some of the most fundamental biochemical reactions in living organisms. In plants it is the source of oxygen evolved in photosynthesis and the source of hydrogen for the reduction of carbon dioxide. The high solubility of carbon dioxide in water, and the dissociation of carbonic acid in water, allow the development of the most important biological buffer system, the bicarbonate system. In animals, water takes part in countless hydration reactions when macromolecules are reduced to their simpler components and it is the final product formed in the acceptance by oxygen of electrons in the cytochrome system.

The melting and boiling points of water are such that it occurs as a solid

and a gas, but mostly as a liquid at the ambient temperatures which prevail over our planet's surface. Most living organisms have evolved to function within the temperature range at which water is liquid and plants and animals that have to survive outside this range are obliged to synthesise special compounds such as cryoprotectants (see Chapter 1). Because of the unusual hydrogen bonding and van der Waals' forces operating between water molecules in a liquid state, water attains its maximum density at 4 °C. This property allows liquid water to accumulate at the bottom of ponds whereas colder water present at the surface may freeze solid. In this way many forms of aquatic life are able to survive winters in a fluid medium.

Aquatic life also makes use of another important physical property of water, namely its very high surface tension. Small arthropods, possessing an exoskeleton that is strongly hydrophobic may be supported above the surface and will be able to locomote, like gerrids, on the surface of the water. Edney (1977) points out that small hydrophilic insects living beneath the surface of the water, but still dependent on atmospheric air, would experience great difficulty in piercing the water surface were it not for the presence of hydrophobic hairs at strategic positions on their body surfaces (e.g. surrounding the tip of the siphon in mosquito larvae).

We must now consider the vapour phase of water and understand the important difference between relative humidity, water vapour pressure and water activity. Water vapour in the air will exert, like any other gas, a pressure proportional to the concentration of water molecules in that gas system. This is known as the water vapour pressure or partial pressure of the water vapour. The higher the kinetic energy (temperature) of the gas system the more water molecules it is able to accommodate (see Fig. 2.2). Biologists are frequently interested in the 'drying capacity' of air and for this reason calculate the difference between the actual or measured water vapour pressure (P) and the water vapour pressure of the same air at the same temperature when fully saturated with water vapour (P_s, see Table 2.2). Thus $P_s - P$ is a useful measure of the potential drying capacity of the air surrounding an animal with a temperature equal to air temperature, and is referred to as the 'saturation deficit'. If the animal's temperature is higher than air temperature, the saturation deficit should not be used as the definitive measurement of the drying potential of air, because the vapour pressure of water on the animal's surface can be higher than the saturated water vapour pressure of the air (Lowry, 1969).

Relative humidity (RH) is not an absolute measure of how much water there is in air. It is the ratio P/P_s, often expressed as a percentage. If we now examine the graphs in Fig. 2.2 more closely it is evident that, although commonly used, RH can be a very misleading measure, when considering the effect of water in air on animals, because the vapour pressure increases curvilinearly with temperature at a fixed RH (see curves A and B). Two environments with the same RH do not necessarily have the same amount of

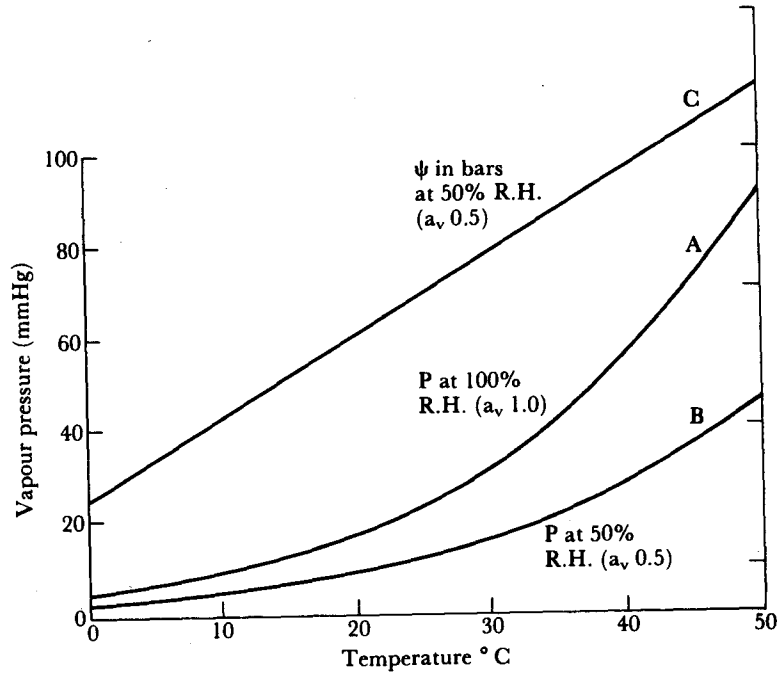


Figure 2.2 The amount of water contained in air at any one relative humidity (RH) or water vapour activity (a_v), increases exponentially with temperature (see curves A and B). Notice how much vapour pressure, and therefore saturation deficit, changes over the temperature range without any change in RH. Redrawn from Edney (1977).

water in the air. Note also from Fig. 2.2. that although the RH differences remain the same between curves A and B over the temperature range (namely 50% RH), the actual vapour pressure differences are small at low temperatures but very large at high temperatures. It is a vapour pressure difference that determines the direction and rate of water vapour movement. Edney (1977) has applied these principles to a practical example showing that water vapour in air on the surface of the desert, even though it is contained in air at a higher temperature and lower RH, will actually move into a cool scorpion burrow where the air is at a lower temperature and higher humidity (Fig. 2.3). The reason becomes clear when one calculates the vapour pressure differences. The same principle holds true for Edney's example of water vapour condensing on the cool surface of a lake (Fig. 2.3).

Considering that it is generally an inappropriate measure of air–water content, it is a pity that biologists (and meteorologists) have become accustomed to using RH, rather than vapour pressure, to describe how much water vapour there is in air. However, there is one circumstance in which RH

Table 2.2 Vapour pressure of water below 100 °C. Pressure of aqueous vapour over water in mmHg for temperatures from −15.8 to 100 °C. Values for fractional degrees between 50 and 89 were obtained by interpolation. (Reproduced with permission of CRC Press Inc. Boca Raton, Florida)

Temperature (°C)	0.0	0.2	0.4	0.6	0.8	Temperature (°C)	0.0	0.2	0.4	0.6	0.8
−15	1.436	1.414	1.390	1.368	1.345	42	61.50	62.14	62.80	63.46	64.12
−14	1.560	1.534	1.511	1.485	1.460	43	64.80	65.48	66.16	66.86	67.56
−13	1.691	1.665	1.637	1.611	1.585	44	68.26	68.97	69.69	70.41	71.14
−12	1.834	1.804	1.776	1.748	1.720						
−11	1.987	1.955	1.924	1.893	1.863	45	71.88	72.62	73.36	74.12	74.88
						46	75.65	76.43	77.21	78.00	78.80
−10	2.149	2.116	2.084	2.050	2.018	47	79.60	80.41	81.23	82.05	82.87
−9	2.326	2.289	2.254	2.219	2.184	48	83.71	84.56	85.42	86.28	87.14
−8	2.514	2.475	2.437	2.399	2.362	49	88.02	88.90	89.79	90.69	91.59
−7	2.715	2.674	2.633	2.593	2.553						
−6	2.931	2.887	2.843	2.800	2.757	50	92.51	93.5	94.4	95.3	96.3
						51	97.20	98.2	99.1	100.1	101.1
−5	3.163	3.115	3.069	3.022	2.976	52	102.09	103.1	104.1	105.1	106.2
−4	3.410	3.359	3.309	3.259	3.211	53	107.20	108.2	109.3	110.4	111.4
−3	3.673	3.620	3.567	3.514	3.461	54	112.51	113.6	114.7	115.8	116.9
−2	3.956	3.898	3.841	3.785	3.730						
−1	4.258	4.196	4.135	4.075	4.016	55	118.04	119.1	120.3	121.5	122.6
						56	123.80	125.0	126.2	127.4	128.6
−0	4.579	4.513	4.448	4.385	4.320	57	129.82	131.0	132.3	133.5	134.7
						58	136.08	137.3	138.5	139.9	141.2
0	4.579	4.647	4.715	4.785	4.855	59	142.60	143.9	145.2	146.6	148.0
1	4.926	4.998	5.070	5.144	5.219						
2	5.294	5.370	5.447	5.525	5.605	60	149.38	150.7	152.1	153.5	155.0
3	5.685	5.766	5.848	5.931	6.015	61	156.43	157.8	159.3	160.8	162.3
4	6.101	6.187	6.274	6.363	6.453	62	163.77	165.2	166.8	168.3	169.8
						63	171.38	172.9	174.5	176.1	177.7
5	6.543	6.635	6.728	6.822	6.917	64	179.31	180.9	182.5	184.2	185.8
6	7.013	7.111	7.209	7.309	7.411						
7	7.513	7.617	7.722	7.828	7.936	65	187.54	189.2	190.9	192.6	194.3
8	8.045	8.155	8.267	8.380	8.494	66	196.09	197.8	199.5	201.3	203.1
9	8.609	8.727	8.845	8.965	9.086	67	204.96	206.8	208.6	210.5	212.3
						68	214.7	216.0	218.0	219.9	221.8
10	9.209	9.333	9.458	9.585	9.714	69	223.73	225.7	227.7	229.7	231.7
12	10.518	10.658	10.799	10.941	11.085	70	233.7	235.7	237.7	239.7	241.8
13	11.231	11.379	11.528	11.680	11.833	71	243.9	246.0	248.2	250.3	252.4
14	11.987	12.144	12.302	12.462	12.624	72	254.6	256.8	259.0	261.2	263.4
						73	265.7	268.0	270.2	272.6	274.8
15	12.788	12.953	13.121	13.290	13.461	74	277.2	279.4	281.8	284.2	286.6
16	13.634	13.809	13.987	14.166	14.347						
17	14.530	14.715	14.903	15.092	15.284	75	289.1	291.5	294.0	296.4	298.8
18	15.477	15.673	15.871	16.071	16.272	76	301.4	303.8	306.4	308.9	311.4
19	16.477	16.685	16.894	17.105	17.319	77	314.1	316.6	319.2	322.0	324.6
						78	327.3	330.0	332.8	335.6	338.2
20	17.535	17.753	17.974	18.197	18.422	79	341.0	343.8	346.6	349.4	352.2
21	18.650	18.880	19.113	19.349	19.587						
22	19.827	20.070	20.316	20.565	20.815	80	355.1	358.0	361.0	363.8	366.8
23	21.068	21.324	21.583	21.845	22.110	81	369.7	372.6	375.6	378.8	381.8
24	22.377	22.648	22.922	23.198	23.476	82	384.9	388.0	391.2	394.4	397.4
						83	400.6	403.8	407.0	410.2	413.6
25	23.756	24.039	24.326	24.617	24.912	84	416.8	420.2	423.6	426.8	430.2
26	25.209	25.509	25.812	26.117	26.426						
27	26.739	27.055	27.374	27.696	28.021	85	433.6	437.0	440.4	444.0	447.5
28	28.349	28.680	29.015	29.354	29.697	86	450.9	454.4	458.0	461.6	465.2
29	30.043	30.392	30.745	31.102	31.461	87	468.7	472.4	476.0	479.8	483.4
						88	487.1	491.0	494.7	498.5	502.2
30	31.824	32.191	32.561	32.934	33.312	89	506.1	510.0	513.9	517.8	521.8
31	33.695	34.082	34.471	34.864	35.261						
32	35.663	36.068	36.477	36.891	37.308	90	525.76	529.77	533.80	537.86	541.95
33	37.729	38.155	38.584	39.018	39.457	91	546.05	550.18	554.35	558.53	562.75
34	39.898	40.344	40.796	41.251	41.710	92	566.99	571.26	575.55	579.87	584.22
						93	588.60	593.00	597.43	601.89	606.38
35	41.175	42.644	43.177	43.595	44.078	94	610.90	615.44	620.01	624.61	629.24
36	44.563	45.054	45.549	46.050	46.556						
37	47.067	47.582	48.102	48.627	49.157	95	633.90	638.59	643.30	648.05	652.82
38	49.692	50.231	50.774	51.323	51.879	96	657.62	662.45	667.31	672.20	677.12
39	52.442	53.009	53.580	54.156	54.737	97	682.07	687.04	692.05	697.10	702.17
						98	707.27	712.40	717.56	722.75	727.98
40	55.324	55.91	56.51	57.11	57.72	99	733.24	738.53	743.85	749.20	754.58
41	58.34	58.96	59.58	60.22	60.86						
						100	760.00	765.45	770.93	776.44	782.00
						101	787.57	793.18	798.82	804.50	810.21

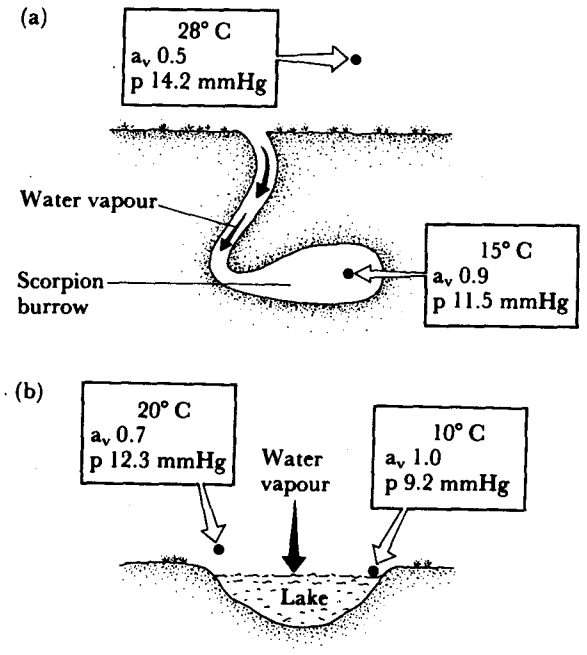


Figure 2.3 (a) Even if the relative humidity inside a scorpion burrow is higher than outside, water vapour will move inwards if the temperature is sufficiently low inside the burrow. (b) In spite of air at the surface of a lake being saturated with water vapour, its vapour pressure may be lower than that of the air above it so water vapour will condense on the lake. Redrawn from Edney (1977).

is the appropriate variable. Some animals and plants take up water from air using hygroscopic salts or concentrated electrolyte solutions. In this case, it is indeed the RH of the air that determines whether the water vapour in it is accessible to the organism.

2.2 Physics of water movement

The movement of water and of solutes in and out of fluid compartments is an exceedingly complex subject but our purpose will be served by reviewing a few key principles.

The rate of diffusion of water can be described by Fick's well-known diffusion equation in its simplest form:

$$\frac{ds}{dt} = -DA\frac{dc}{dx}$$

where ds/dt is the instantaneous rate of movement of substance; D the diffusion coefficient, which is a measure of the ease of diffusion, for example

the permeability of the membrane; A the diffusion area; and dc/dx the concentration gradient of the substance moving (moles per unit distance). We conclude that, in a way analogous to heat exchange, the rate of diffusion is largely governed by the diffusion area involved but, instead of temperature gradients, concentration gradients are the driving forces.

Osmosis, the movement of solvent between solutions, is also a complex physical process and opinions differ among physical chemists about the exact mechanisms involved. A highly simplified kinetic model, however, will be used as our example. In this model we assume that the molecules of both solvent and solute are perfectly round spheres and there are two solutions separated by a thin and ideally semi-permeable membrane. Then according to Fig. 2.4A, because of the higher water concentration on the left-hand side, the number of random collisions of the water molecules with the membrane per unit area and per unit time will be greater on the left-hand side than on the right-hand side of the membrane. This difference will result in a net flow of water from left to right.

The mechanism illustrated in Fig. 2.4A does not easily explain the fact that osmotic permeability often exceeds diffusion permeability. Rankin and Davenport (1981) offer a possible explanation for this difference. They suggest that osmotic water flow does not occur by random diffusion as depicted in Fig. 2.4A, but via membrane pores shown in Fig. 2.4B. These pores are water-filled and a pressure gradient is set up within them, down which the water molecules will pass. The motion of molecules along the pore becomes more ordered and less random.

Passive diffusion, which we have been describing, is a simple form of transport during which no energy is released. The process depends on the kinetic energy of the substances involved and takes place down electrochemical gradients until equilibrium is reached on both sides of the membrane. *Active transport* occurs when substances are transported against electrochemical gradients. The exact process is still not fully understood but involves the continual expenditure of energy, mostly derived from the metabolism of ATP. Carrier molecules also appear to play an important role in this process as they can combine reversibly with many substances being transported across membranes.

When discussing actual animal examples we shall emphasise that water itself is never actively transported but on occasion the osmotic gradient is altered in such a way that water appears to move against it. One of the most dramatic examples of this phenomenon is provided by rectal reabsorption of water in insects, which we shall discuss later. As a basis for understanding the possible mechanisms involved in rectal reabsorption, the transport mechanisms across an epithelial cell in Fig. 2.5 should be studied. Active transport of Na^+ leads to a high osmotic concentration within the infolding. Water is then drawn osmotically into the infolding and the increased hydrostatic pressure results in a bulk flow of liquid into the tissue fluid.

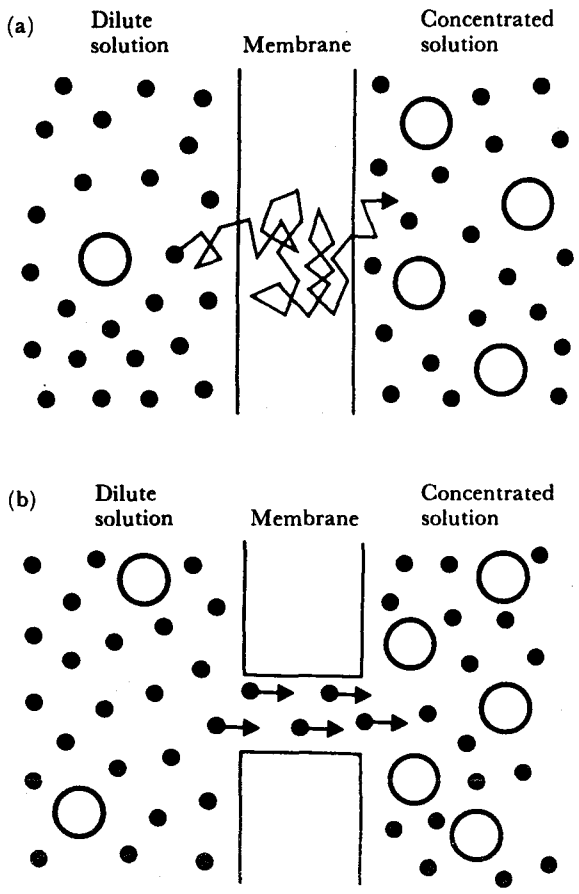


Figure 2.4 (a) A simplified model of passive diffusion of water molecules from a dilute to a concentrated solution (●, water; ○, solute). (b) Uniform flow of water molecules through a membrane pore during osmosis. Redrawn from Rankin and Davenport (1981).

2.3 Terminology

To facilitate the reading of texts and papers, the following elementary terminology should be understood.

Today, the concentration of chemical solutions is almost universally expressed in *molarity*. A 1 *molar* solution contains 1 mole of solute per litre of solution and a 1 *molal* solution contains 1 mole of solute dissolved in 1 kg of solvent. In dilute aqueous solutions the numerical difference between molarity and molality is small but in concentrated solutions it becomes significant. Osmotic concentrations in the tissue fluids of animals are usually expressed

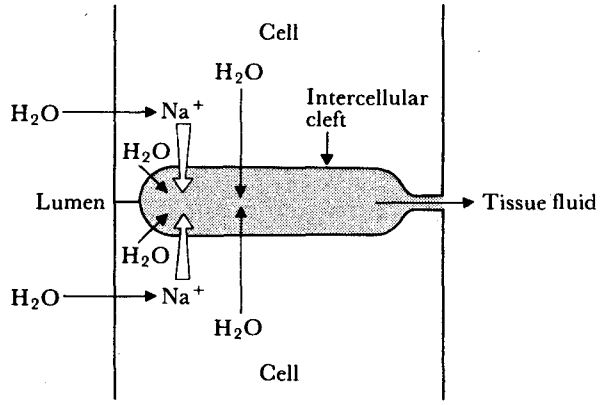


Figure 2.5 A model depicting the transport of water via the intercellular cleft of an epithelial cell. Water follows the active transport of Na^+ and as the volume of the cleft does not change appreciably, water is transported into the tissue fluids. Modified from Schmidt-Nielsen (1983).

in osmoles (1 molal = 1 osmole). Because osmotic activity depends on the number of particles in solution, osmolality depends on the molality of a solution as well as the extent to which the solute dissociates. The osmolality of a NaCl solution, for example, theoretically should be twice the molality, though in practice the dissociation is never complete. Tables are available for calculating the osmolality of electrolyte solutions. The osmolality of sea water is about 1000 mosmol kg^{-1} and that of mammalian plasma about 300 mosmol kg^{-1}.

Osmotic concentrations are usually measured indirectly by measuring another colligative property of the solution, such as depression of vapour pressure or depression of the freezing point. Instruments are available which measure freezing point or vapour pressure depression automatically and provide a direct digital readout in milliosmoles per kilogram.

If two solutions have the same osmotic concentrations they are described as being *iso-osmotic*. If the osmotic concentration of one is lower than a reference solution it is said to be *hypo-osmotic*, whereas the reference solution is now described as being *hyperosmotic* to the former solution. The terms isotonic, hypertonic and hypotonic encountered in medical texts are less precise and should not be used.

Some marine invertebrates, particularly those living in estuaries where the osmotic concentration of the external medium fluctuates with the tide, do not regulate the total osmotic concentration of their internal tissue fluids, so that the osmotic concentration of their tissue fluids is the same as that of the external medium; they are called *osmoconformers*. If they are also able to tolerate a wide range of salinities they are described as being *euryhaline*. In

contrast, an animal which cannot tolerate a wide range of salinities is known as *stenohaline*. Animals which regulate the osmotic concentration of their body fluids are known as *osmoregulators*. By combining this terminology with that of the chapter on temperature we can come up with some rather overwhelming jargon, e.g. *homeothermic, ectothermic, stenohaline osmoregulator*, which is a reasonable description of a fast swimming tuna fish.

2.4 The measurement of evaporative water loss and water turnover rates

The simplest method of determining water loss from an animal is to weigh the animal over specific time periods and account for all other avenues of weight loss. For example, if the animal does not defecate or urinate, the major measured weight loss would be the result of evaporative water loss (EWL). Admittedly, the animal will also be losing carbon in the form of CO_2, which is usually ignored but can be measured by analysing the gas exchange of the animal or estimated from the metabolic rate. This so-called 'gravimetric' or weighing method generally requires only the simplest apparatus. However, very precise electronic balances are available today which allow the investigator to record the weight of large animals continuously and accurately. They are specially dampened so that movements of the animals are electronically compensated. These balances have been used to record the weight of large mammals standing in direct sunlight under hot conditions and also that of men pedalling exercise bicycles. The continuous loss in weight which is recorded is the result of EWL from sweating and/or thermal panting, provided that defecation and urination are taken into account.

The gravimetric method does not provide a minute-by-minute estimate of water loss from animals, which is a distinct disadvantage to those biologists interested in relating a specific activity of an animal with rates of EWL. To measure EWL instantaneously, use is made of modern electronic sensors which are very sensitive to ambient water vapour. These sensors can be placed downstream of an animal in an enclosed space, and continuous measurements made of the temperature and RH of the excurrent air. These measurements then can be compared with the temperature and RH of the excurrent air when no animal is present in the system, or an additional sensor can be incorporated into the system upstream of the animal enclosure for comparative purposes. By subtracting the water vapour in the incoming stream from that in the excurrent stream, the water vapour lost from the animal can be calculated (Fig. 2.6). The amount of water vapour in the air can be calculated from the temperature and vapour pressure (or RH) using appropriate tables (*Handbook of Physics and Chemistry*) (see Table 2.3).

Both of the described methods for measuring EWL have the very real disadvantage that the animals employed in these experiments must be restrained under artificial laboratory conditions. It is, however, possible to

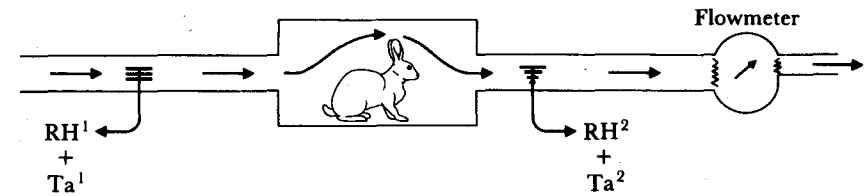


Figure 2.6 By measuring the relative humidity and temperature of the incurrent and excurrent air, as well as the flow rate over the animal, the evaporative water loss of the animal can be measured instantaneously.

Table 2.3 Weight in grams of a cubic metre of saturated aqueous vapour (from Smithsonian Tables). (Reproduced with permission of CRC Press, Boca Raton, Florida)

Temperature °C	0.0	1.0	2.0	3.0	4.0	5.0	6.0	7.0	8.0	9.0
−20	1.074	0.988	0.909	0.836	0.768	0.705	0.646	0.592	0.542	0.496
−10	2.358	2.186	2.026	1.876	1.736	1.605	1.483	1.369	1.264	1.165
−0	4.847	4.523	4.217	3.930	3.660	3.407	3.169	2.946	2.737	2.541
+0	4.847	5.192	5.559	5.947	6.360	6.797	7.260	7.750	8.270	8.819
+10	9.399	10.01	10.66	11.35	12.07	12.83	13.63	14.84	15.37	16.21
+20	17.30	18.34	19.43	20.58	21.78	23.05	24.38	25.78	27.24	28.78
+30	30.38	32.07	33.83	35.68	37.61	39.63	41.75	43.96	46.26	48.67

measure total water turnover rate, though not EWL separately, in the field by using isotope dilution techniques. The most commonly used isotope is tritium (^3H). When tritiated water (^3HOH) is injected into an animal it soon mixes with the natural water pool of the body and its concentration in the body fluids reaches equilibrium. As time proceeds the isotope disappears from the tissue fluids and if this rate of disappearance or wash-out time is measured, the rate of water turnover in the whole animal can be estimated. In practice, the animal is captured and injected with a known dose of ^3HOH. Serial blood samples are then taken over several hours until the isotope has become equilibrated. The animal is then released to behave normally in the field under natural conditions before being recaptured at predetermined intervals for blood sampling and eventual calculation of the water turnover rate (Fig. 2.7).

2.5 Water balance

Whenever one is confronted with the task of evaluating the water relations of an animal, it is advisable to do so by a systematic examination of the water balance, which depicts all the possible avenues of loss and gain (Fig. 2.8). Water balance has been described by Maloiy *et al.* (1979) as an open flow-

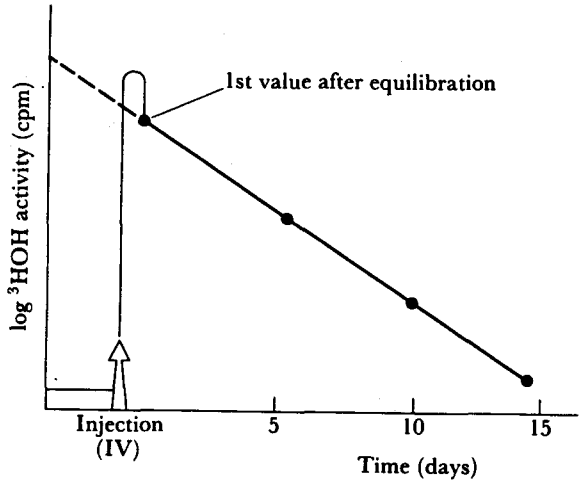
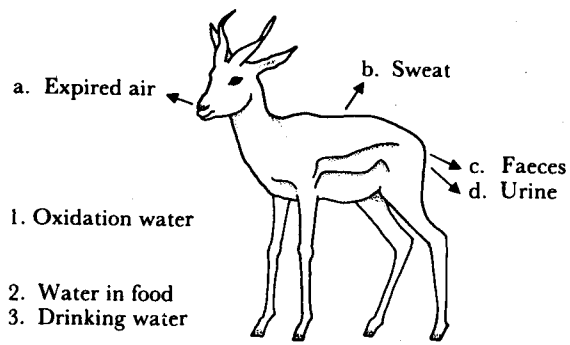


Figure 2.7 Rate of disappearance of tritiated water (^{3}HOH) from the body fluids of a mammal (arbitrary units). The water turnover rate is then calculated from the rate of disappearance of the isotope.



Gain		Loss
1. Oxidation water		a. Evaporation from lungs
2. Water in food	=	b. Evaporation from skin
3. Drinking water		c. Water in faeces
		d. Water in urine

Figure 2.8 Water balance model for a typical mammal, the springbok.

through system. Water enters the system as drinking water, as preformed water in the food and as the water of oxidation (or metabolic water). Water is lost in the urine, faeces and milk and as vapour from the respiratory system and surface of the body. Disturbances in the balance can occur from hour to hour or over several months, depending on the species and the environmental conditions. Negative balances can reach as high as 40% of total body

weight in tolerant species, while in some mammals, including man, a loss of 15% can be life threatening. The distribution of water within the various body-fluid compartments also varies, depending upon the degree of dehydration experienced by the animals. For example, in most ungulates dehydration causes a marked reduction in the water contained in the gastrointestinal tract, the reduction being more severe in sheep and goats than in cattle. The decline in interstitial fluid is less severe but again more marked in sheep than in cattle. In contrast, the water content of the plasma compartment is homeostatically well controlled and undergoes relatively little change during mild dehydration. The opposite situation exists in insects, where the haemolymph (blood) acts as a water reservoir for the tissues.

The type of water balance depicted in Fig. 2.8 is applicable to most mammalian herbivores, but additional avenues of loss and gain must be incorporated if the lower vertebrates and insects are to be considered. In certain birds and reptiles, water loss via salt glands must be considered, while in social insects the phenomenon of trophallaxis, in which members of the same colony feed one another a liquid diet, must be accounted for. In addition, certain insects lose water via repugnatorial glands and when laying pheromone trails. The remarkable ability of certain insects, such as booklice (Psocoptera), to absorb water vapour from unsaturated air, is an additional avenue of gain which must be included.

The major environmental factors influencing water loss in living organisms have been reviewed by Louw and Seely (1982): These are radiation, ambient temperature, the water vapour deficit or saturation deficit and wind speed. All these factors interact with one another and with the inherent behaviour, morphology and physiology of the species in question. In practice, under conditions of high ambient temperature, low vapour pressure, and high wind speed, water loss from animals will be high, especially if the animals exercise. In response to such conditions the animal may be able to increase its intake of free drinking water and reduce water loss via the faeces and urine, or reduce activity.

Before leaving the water balance of animals we should consider the most interesting balance between the production of metabolic water on the one hand and total water loss on the other, because animals that are able to survive without drinking water on a dry diet must produce sufficient metabolic water to equal the amount they lose via all available avenues. Adaptations to ensure such a positive water balance must therefore overcome the problem inherent in the fact that metabolic water production requires oxygen, and delivery of oxygen to the respiratory surface of most terrestrial animals entails water loss via exhaled gases. According to Taylor (1969) large desert antelope such as the oryx overcome this problem by breathing more deeply and not more rapidly. In this way more oxygen is supplied to the alveoli allowing formation of more metabolic water, without greatly increasing the ventilation rate of the dead space in the respiratory system. Taylor (1969)

has estimated that under cool night-time conditions the oryx will approach a positive water balance as a result of its increased metabolic rate and slow deep breathing, if the RH of the inspired air does not fall below about 70%. The economics of metabolic water formation is a fascinating problem in ecophysiology but requires far more careful experimentation before exact threshold values can be assigned to different species.

Positive water balances, however, could theoretically ensue from metabolic water production, provided water loss is minimised by suitable adaptations in the following kinds of circumstances, thereby allowing survival without access to free water.

1. Very high metabolic rate plus low respiratory water loss, e.g. flying insect such as carpenter bee.
2. High metabolic rate plus moderate respiratory water loss, e.g. desert rodent in burrow.
3. Very low metabolic rate plus extremely low respiratory water loss, e.g. desert scorpion.
4. Moderate metabolic rate plus moderate respiratory loss, e.g. desert ostrich.
5. Low requirement for metabolic water as a result of large amounts of preformed water in the diet, e.g. gorilla.

The importance of environmental factors such as temperature and vapour pressure in favouring a positive balance are also obvious and well illustrated by Weis-Fogh's (1967) studies at Cambridge on flying locusts. He demonstrated that during level flight a locust would use 270 J g^{-1} h^{-1} of metabolic power and, if fat were the sole fuel, it would produce 7.28 mg water g^{-1} h^{-1} of metabolic water. Thoracic ventilation rate in a resting locust is about 30 ml air g^{-1} h^{-1} and rises to 320 ml g^{-1} h^{-1} during flight. Whether or not the locust will remain in a positive water balance during flight will depend on the temperature, radiation load and the RH of the inspired air. Weis-Fogh combined these three variables in a graphic model to describe the ambient conditions which would allow locusts to fly in a positive water balance (Fig. 2.9). He concluded that a locust swarm which was lifted by thermal currents from ground level (T_a, 35 °C) to an altitude of 3 km (23 °C) would be capable of sustained flight in positive water balance if the RH remained above the moderate level of 35%. When the large swarms of these highly destructive insects fly great distances across major desert areas of Africa, they are therefore not likely to be compromised by lack of water.

Weis-Fogh's type of calculation requires more detailed information than is normally available. To estimate the amount of metabolic water production when such information is not available, use can be made of the respiratory quotient (RQ) and estimates of food consumption or energy expenditure. The relationship between substrate oxidised, O_2 consumption, RQ, energy and metabolic water produced is summarised in Table 2.4. Note that

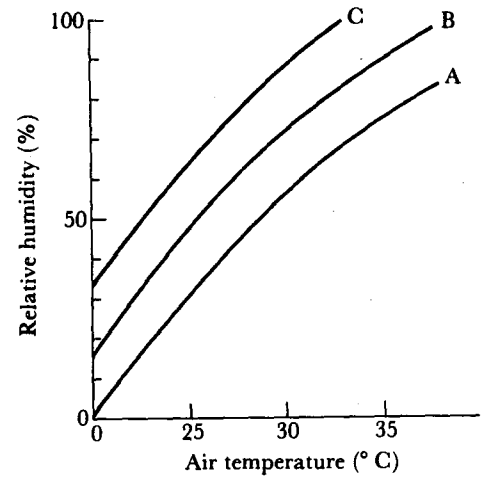


Figure 2.9 Each curve represents a combination of ambient temperatures and humidities at which water loss by a flying locust is balanced by the production of metabolic water. A, no net radiation load; B and C, thoracic temperature theoretically increased by 2 and 4 °C respectively through solar radiation. Redrawn from Weis-Fogh (1967) and Edney (1977).

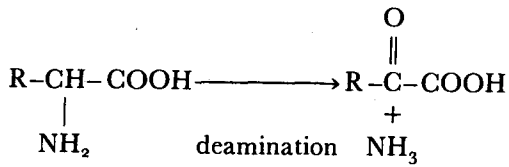
Table 2.4 Relationship between the respiratory quotient (RQ), metabolic water production and energy production when the major nutrients are oxidised. From Prosser (1973) and Schmidt-Nielsen (1983)

Food	RQ	g water g food^{-1}	l O_2 g food^{-1}	l O_2 g water^{-1}	kJ g food^{-1}	g water kJ^{-1}
Carbohydrates	1.0	0.56	0.83	1.49	17.4	0.0320
Fats	0.71	1.07	2.02	1.89	39.7	0.0269
Proteins	0.79	0.40	0.97	2.44	17.4	0.0228

although fats produce far more energy and metabolic water per gram of substrate than carbohydrates, they actually produce less metabolic water per kilojoule of energy produced. This fact is often overlooked by biologists particularly when speculating on adaptive shifts in the substrate being metabolised to produce more metabolic water.

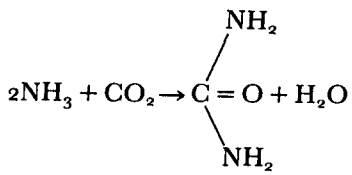
2.6 Nitrogen excretion

Because protein catabolism occurs in all animals, the problem of excreting the nitrogenous end-products of this catabolism is universal:



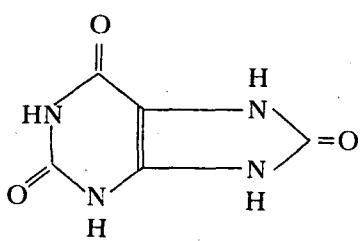
After deamination of the protein the α-ketoacid formed can be fully oxidised to CO_2 and H_2O and excreted through the respiratory and integumentary systems. The NH_3 radical, however, is toxic and is not so easily handled in terrestrial animals. In aquatic animals the NH_3 itself is excreted rapidly into the surrounding water, in which it is highly soluble. These animals are known as *ammonotelic*.

In many animals, including certain aquatic forms, the NH_3 radical is first changed to urea before it is excreted:



Urea is far less toxic than ammonia and some animals, such as elasmobranchs, can tolerate very high concentrations in their tissues. They use the raised urea concentration of their tissue fluids, which exceeds that of the surrounding sea water, to allow water to enter their tissues by osmosis. Special adaptations are necessary, however, to be able to tolerate these concentrations. Some animals switch during their lifetime from being ammonotelic (tadpole) to become ureotelic (adult frog).

The excretion of urea requires the concurrent excretion of a considerable amount of water. Animals that use uric acid as the obligatory end-product for nitrogen excretion enjoy an advantage in dry environments, as uric acid is very insoluble in water and can be excreted in the form of a solid paste or even a dry pellet. The molecular structure of uric acid is more complex than that of urea and requires considerably more energy for its synthesis than urea does:



Uric acid is seldom, if ever, excreted as the acid, but rather in the form of a urate salt and the excretion of uric acid (*uricotelism*) is really urate excretion. Rankin and Davenport (1981) have assembled data on the nitrogenous excretion of Chelonia (tortoises and turtles) to demonstrate how habitat can influence the pattern of obligatory nitrogen excretion even within one order of vertebrates (see Table 2.5).

Table 2.5 **Nitrogen excretion in chelonia. From Rankin and Davenport (1981)**

		% of urinary nitrogen		
Species	Habitat	Ammonia	Urea	Urate
Chrysemys scripta	Freshwater	79	17	4
Kinixys erosa	Moist terrestrial	6	61	4
Testudo graeca	Dry terrestrial	4	22	52
Gopherus berlandieri	Desert	4	3	93

Table 2.5 cautions us not to be too hasty in assigning nitrogen excretory patterns to different groups of animals. Nevertheless, a broad pattern of excretion does exist:

Aquatic invertebrates	ammonotelic
Insects	uricotelic
Spiders	guanine
Teleost fish	ammonotelic and ureotelic
Elasmobranchs	ureotelic
Amphibians	ammonotelic, ureotelic and uricotelic
Birds and reptiles	uricotelic
Mammals	ureotelic.

Because it is a reasonably small, soluble, molecular particle urea is active osmotically. Though the elasmobranchs can use the osmotic activity to advantage, it would disrupt the osmotic balance of reptilian and avian embryos developing within cleidoic (boxed-in) eggs. Consequently these embryos are uricotelic.

2.7 Excretion mechanisms

The physiology of the various excretory mechanisms in animals such as kidney function, the role of contractile vacuoles, Malphigian tubules in insects and salt glands in reptiles and birds are beyond the scope of this text. For a very readable account of these mechanisms the reader is referred to Rankin and Davenport (1981).