Chapter 5

Temperature

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The pile, or 'fur', on the thorax of the moth is effective insulation.
(Photograph courtesy of P. Withers and T. Stewart, Zoology Department, The University of Western Australia.)

T he body temperature (T_b) of active animals ranges from about $-2°$ C to $+50°$ C, although some can survive at lower ●●●●● or higher temperatures in an inactive (dormant) state. A few animals can survive extremely low body temperatures (e.g., $-200°$ C) and some can survive moderately elevated temperatures (60 to 70° C).

The body temperature of many animals is similar to the **ambient**, or air, temperature (T_a). Other animals, however, raise their body temperature above T_a and may precisely regulate T_b by either behavioral or physiological means.

Body temperature has a profound effect on the physiology of animals. Let us first consider the physical effects of temperature on physiology, and then let us examine the mechanisms for heat exchange between an animal and its environment and the regulation of heat exchange.

Physical Effects of Temperature

Temperature Scales

Temperature is a measure of the average thermally induced molecular motion; molecules vibrate faster at higher temperatures. Our sensory system provides us with a qualitative indication of temperature. An object may feel "hot" or "cold" to our touch, but this thermal sensory information is subjective, qualitative, and unreliable! Consider the sensation when we remove a metal tray of ice cubes from a freezer; the metal tray feels "colder" than the ice cubes, although both are at the same temperature. This is because the metal tray conducts heat better than ice, and our hand loses heat faster to the metal than to ice. Our sensory perception of temperature is thus biased by the rate of heat transfer.

Thermometers are mechanical, electrical, or optical devices that measure temperature. They measure some physical material property that is a function of temperature, rather than temperature *per se*, e.g., a change in volume of a liquid (mercury or alcohol thermometer), a change in length of a solid (bimetallic strip), a change in voltage across a junction of two dissimilar metals (thermocouple), or a change in emitted radiation (pyranometer).

There are a number of temperature scales. The SI unit for temperature is the degree Kelvin, or K (named after Lord Kelvin). The Celsius (or centigrade) scale defines 0° C as the freezing point of pure water and 100° C as the boiling point of water (at standard pressure); this scale is named

after Anders Celsius. The K scale and C scale are related as follows.

$$°C = °K - 273.15$$
$$°K = °C + 273.15 \quad (5.1a)$$

Absolute zero (0° K $= -273.15$ °C) is the lowest possible temperature; it is the temperature at which thermal motion ceases. Another non-SI temperature scale in common usage is the Fahrenheit scale, °F (named after Gabriel Fahrenheit); the freezing point of water is 32° C and the boiling point is 212° F. Hence,

$$°F = \tfrac{9}{5} °C + 32 \quad (5.1b)$$

Reaction Rates

Temperature is an important and all-pervasive physical property of the environment; it measures the motion and thermal kinetic energy of molecules. The average kinetic energy of molecules is proportional to the absolute temperature. For an ideal gas, the mean kinetic energy (E; J mole^{-1}) is proportional to the temperature (K)
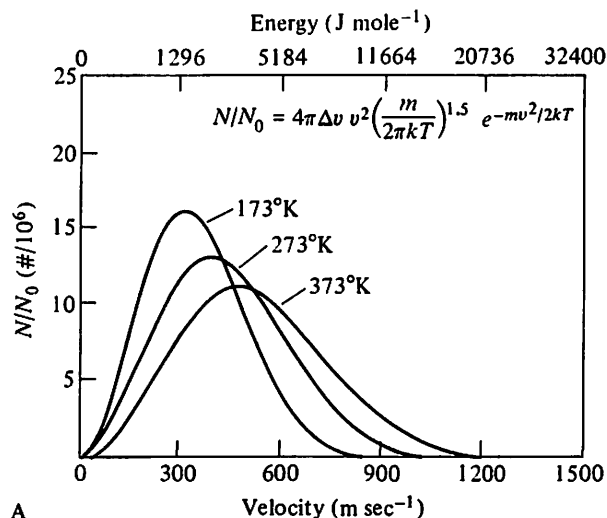
$$E = \tfrac{1}{2}mv^2 = 1.5kT \quad (5.2)$$

where m is the molecular weight, v is the mean molecular velocity (m sec^{-1}), and k is the Boltzmann constant. However, not all molecules at a given temperature have exactly the same kinetic energy. The distribution of energies for molecules in gases or liquids at a particular temperature has a maximum at a specific velocity, and is skewed towards higher velocities and energies (Figure 5–1A).
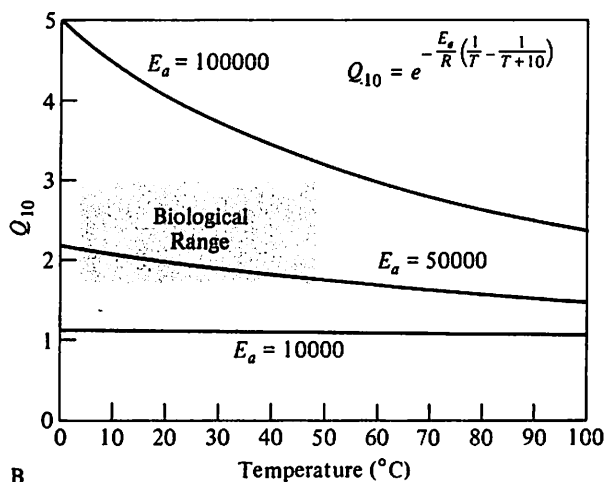
Temperature can have a profound effect on physical, chemical, and biochemical reaction rates as we have already seen (see Chapter 3, page 30). At a given temperature, a certain fraction of molecules have kinetic energy greater than the required **activation energy** (E_a) and react when they collide. The fraction of molecules with velocity/energy greater than any particular value can be calculated from the Maxwellian distribution formula (Figure 5–1A). Alternatively, the specific rate constant, k, can be determined from the Arrhenius equation (see Chapter 3, page 39) and related to temperature as

$$\frac{k_2}{k_1} = e^{-\frac{E_a}{R}\left(\frac{1}{T_1} - \frac{1}{T_2}\right)} \quad (5.3a)$$

where k_2 and k_1 are the reaction rates at temperatures T_2 and T_1, and E_a is the activation energy. The **critical thermal increment**, μ, rather than activation energy, is used to describe the effects of temperature on complex physiological processes such as heart rate, respiratory rate, or metabolic rate.

Energy (J mole^{-1})

$$N/N_0 = 4\pi\Delta v\, v^2\left(\frac{m}{2\pi kT}\right)^{1.5} e^{-mv^2/2kT}$$

A

The ratio k_2/k_1 for a 10° K difference in temperature (from 303° K to 313° K) is often about 2, because E_a is about 50 kJ mole^{-1}. The value for a 10° difference in temperature is the Q_{10}; it can be calculated if the temperature difference is not exactly 10° C as the following.

$$Q_{10} = \frac{k(T + 10)}{k(T)} = (k_2/k_1)^{10/(T_2-T_1)} \quad (5.3b)$$

The Q_{10} should decrease at increasing temperatures (since $1/T - 1/(T + 10)$ is smaller at higher T) and increase with E_a or μ (Figure 5–1B).

B

FIGURE 5–1 (A)   Velocity and energy distribution of air molecules at three temperatures. The number of molecules per 10^6 molecules (N/N_0) was calculated using the Maxwellian energy distribution formula

$$N/N_0 = 4\pi\Delta v\, v^2(m/2\pi kT)^{1.5}e^{-(mv^2/2kT)}$$

where N_0 is the number of molecules (i.e., 10^6), Δv is the velocity range, v is the velocity (m sec^{-1}), m is the molecular weight (7.78 10^{-26} kg molecule^{-1} for air), k is Boltzmann's constant, and T is temperature (°K). **(B)** Q_{10} values calculated as a function of activation energy (E_a: J mole^{-1}) and temperature (°C). The shaded region indicates the approximate biological range.

TABLE 5–1

Q_{10} and activation energy (E_a)/critical thermal increment (μ) for physical, biochemical, and physiological rates. E_a or μ = 0.1 $RT(T + 10)$ ln Q_{10}		
	Temperature (°C)	**Q_{10}**	**E_a/μ** (kJ mole^{-1})

	Temperature (°C)	Q_{10}	E_a/μ (kJ mole^{-1})
Physical Reactions			
Diffusion[1]	20	1.03	—
Biochemical Reactions			
Pyruvate kinase V_{max}			
Rat	>25	1.75	41.9
Rat	<25	3.23	83.7
Cytochrome reductase			
Possum	>20	1.52	33.0
Possum	<20	2.53	64.0
Albumin coagulation	69	635	646
Hemoglobin coagulation	60	13.8	249
Leukocyte heat death	38	28.8	279
Protozoan heat death	36	900–1000	
Physiological Reactions			
Water flea			
Gill movement	5	3.73	87.6
	13	1.72	38.1
Crayfish heart rate	5	2.4	60.3
	10	1.9	44.2
	15	1.6	33.5
	20	1.4	24.8
	25	0.8	− 17.0
	30	0.5	− 54.7
Potato beetle VO_2	10	2.4	60.4
	15	2.5	65.4
	20	2.1	54.8
	25	1.3	20.0
Torpid mammal VO_2	0	2.85	67.3
	10	3.71	90.4
	20	4.11	104.3

[1] $D = RT/6\pi N\eta r$; R = gas constant, T = °K, N = 6.02 10^{23}, η = viscosity, r = radius of diffusing molecule.

The Q_{10} for physical processes, such as diffusion, is about 1. That for biochemical reactions and many physiological rates (e.g., metabolic rate, respiratory rate, heart rate) is typically 2 to 3 (Table 5–1), but often depends on T in a more complex manner than indicated by Equation 5.3b. For example, the Q_{10} for the heart rate of crustaceans is greatest (>3) below 10° C and is about 2 from 10° to 20° C; Q_{10} declines to 1 to 2 at temperatures above 20° C. There is a similar rapid decline in Q_{10} at temperatures above 20° C for the VO₂ of a potato beetle. The gill ventilation rate of a water flea *Daphnia* shows a marked transition in Q_{10} from about 3.7 to about 1.7 at 13° C. The value of μ declines markedly from typical biological values (50 to 60 kJ mole⁻¹) at high temperatures (e.g., *Daphnia* and potato beetle).

The Thermal Environment

The thermal environment of animals is generally complex. Consider, for example, a large lizard in a typical habitat (Figure 5–2). Radiative heat exchange is dominated by direct solar radiation but there is also scattered and reflected solar radiative heat gain and radiative heat gain by long-wave radiation from objects in the environment; the animal loses heat by long-wave radiation from its surface. There is conductive heat transfer between the animal and the ground through the feet and the body if it is pressed to the ground. Convective heat transfer occurs by forced and/or free convection. Evaporative heat loss occurs across the skin and from the respiratory tract. The relative magnitudes of these various avenues for heat gain and loss are determined by the particular biotic and abiotic conditions.

The effective thermal environment is best determined by empirical measurement; this can be accomplished using models of animals placed in the natural environment. The effective environmental temperature depends on air temperature (T_a) and the conductive, convective, and radiative thermal regimens. For example, the environmental temperature is effectively $>T_a$ if there is a significant radiative heat load, and is $<T_a$ if there is a considerable radiative heat loss. The **operative temperature**
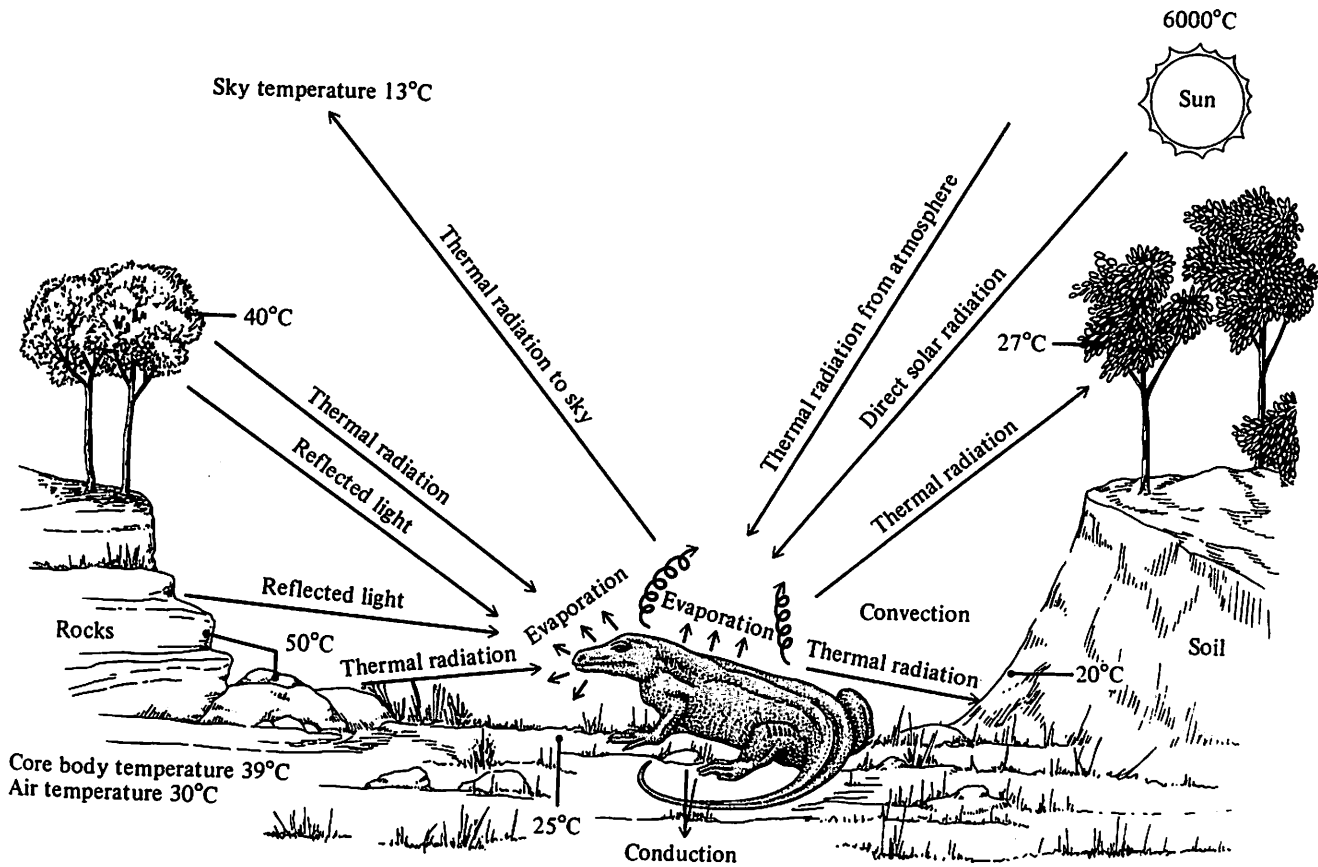

FIGURE 5–2 Representation of conductive, convective, radiative, and evaporative heat exchange for a terrestrial reptile in a typical terrestrial environment. *(From Heatwole and Taylor 1987.)*

(T_e) provides a measure of the effective environmental temperature. It is the temperature of an isothermal (same temperature throughout) black body in an identical conductive, convective, and radiative environment as the animal occupies (Bakken 1980), i.e.,

$$M - E = C_e (T_b - T_e) = C_{es} (T_b - T_{es})   (5.4)$$

where M is metabolic heat production, E is evaporative heat loss, and C_e is the operative thermal

conductance (cf. the nonevaporative total heat transfer coefficient, h; see below). The **standard operative temperature** (T_{es}) is the operative temperature under standardized convective conditions (usually defined as free convection), where C_{es} is the standard operative thermal conductance.

T_{es} and T_e account for the radiative and convective characteristics of the thermal environment. For example, the VO_2 of white-crowned sparrows (*Zonotrichia*) is decreased at low T_a and is increased at high T_a if there is a significant radiative heat load (Figure 5–3A). There is a linear relationship between $(M - E)$ and T_e (Figure 5–3B), as predicted by Equation 5.4 when evaporative heat loss and the
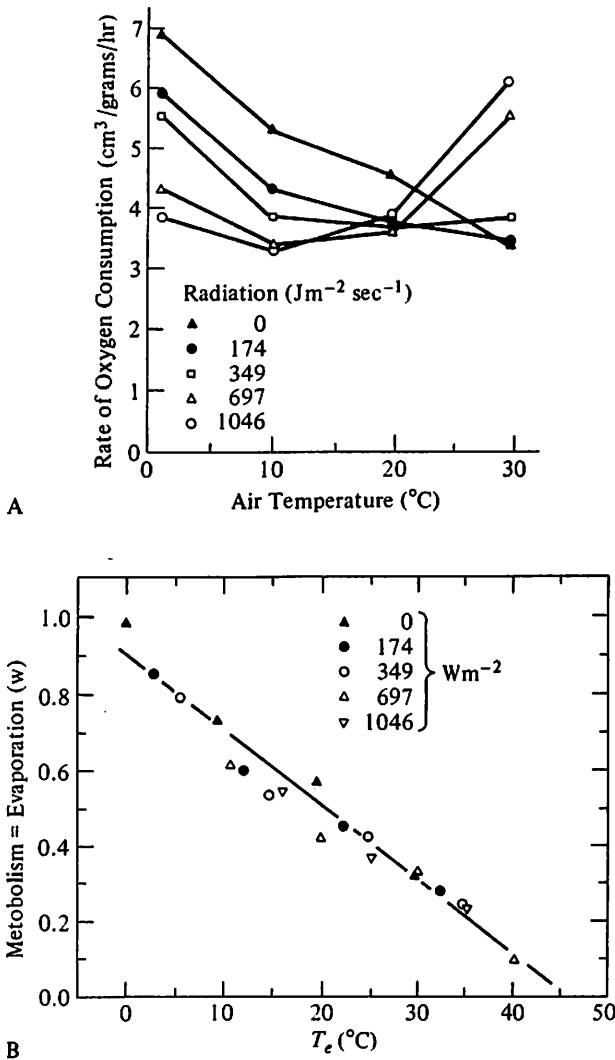

A

FIGURE 5–3 (A) Oxygen consumption rate of the white-crowned sparrow (*Zonotrichia leucophrys*) at varying air temperatures in the absence of near incident infrared radiation (solid triangles) and varying levels of incident IR and visible radiation (other symbols).
(B) Net nonevaporative heat flux (watts) for white-crowned sparrows as a function of operative temperature (T_e). *(From Calder and King 1974; after DeJong 1971; from Bakken 1980.)*
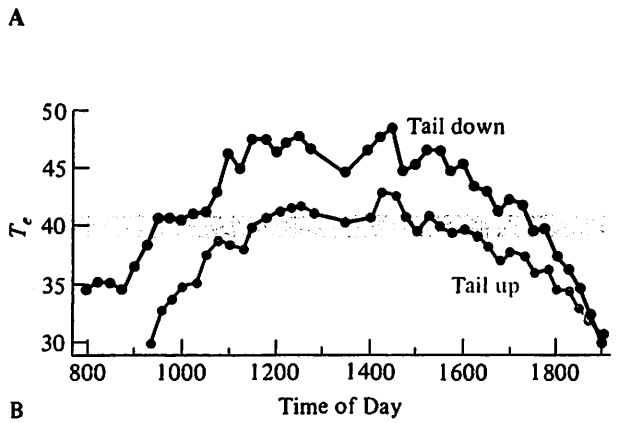

A

FIGURE 5–4 (A) The Cape ground squirrel uses its tail as a 'parasol' to shade its body from direct solar radiation. **(B)** The 'parasol' thermoregulatory behavior of the ground squirrel considerably reduces the operative temperature $(T_e;$ °C) for a model of the ground squirrel. *(Photograph by P. Withers; data from Bennett et al, 1984.)*

convective/radiative regimes are taken into account (convection was free in this example so $T_e = T_{es}$). For the antelope ground squirrel in the Sonoran desert, the T_{es} can rise to 70° C on a hot sunny day; the T_e is less because there is forced convective heat loss, but still reaches about 65° C; air temperature is lower, reaching 55° C (Chappell and Bartholomew 1981).

T_e provides a better index of the actual thermal environmental than does T_a, and T_{es} indicates the potential thermal environment in the absence of forced convection. The Cape ground squirrel uses its tail as a parasol to shade its body from direct solar radiation (Figure 5–4A). This has important thermoregulatory consequences, since shading the body reduces the T_e by about 5° C (Figure 5–4B).

Patterns of Temperature Regulation

Most animals are unable to control their body temperature, and T_b passively conforms to their thermal environment (T_e); these animals **thermoconform**. There must be a thermal gradient between the body and ambient environment for all animals to dissipate the metabolic heat production, but this is biologically insignificant (typically <1° C) for most thermoconformers.

Some animals, in contrast, regulate their body temperature often against a substantial thermal gradient between their body and the environment; they **thermoregulate**. Thermoregulation can be accomplished in essentially two different ways: by either having a high heat gain or a large metabolic heat production. An insulating layer of fur (mammals), feathers (birds), fat (birds and mammals), or chitin hairs (insects) facilitates thermoregulation. Many terrestrial animals thermoregulate by basking in the sun. Birds and mammals, a few reptiles and fish, a number of insects, and even a few plants are able to generate sufficient metabolic heat to thermoregulate.

We must carefully define the terminology for patterns of temperature variation before we examine patterns of body temperature regulation or conformation for different animals. Many of the terms that have been used to describe patterns of body temperature are relative terms and lack a mechanistic basis (Cowles 1940, 1962). "**Cold blooded**" and "**warm blooded**" are poor terms, although, unfortunately, they still are used. We intuitively know what these terms mean; birds and mammals are warm blooded and snails, crabs, and frogs are cold blooded. However, what is the temperature that separates warm from cold blooded? Is a desert snail with a T_b of 40° C cold blooded or warm blooded? Is a hibernating mammal with a T_b of 5° C cold blooded or warm blooded?

The terms **poikilotherm** and **homiotherm** are also vague and ambiguous. A poikilotherm has a variable body temperature (from the greek "poikilos," which means changeable) and a homiotherm has a constant T_b ("homoios" is similar). Again, we intuitively know that snails, crabs, and frogs are poikilotherms and birds and mammals are homiotherms, but a fish that lives deep in the ocean at a constant water temperature is a homiotherm, although not in the same physiological sense that a mammal is a homiotherm. A hibernating mammal can have a markedly variable T_b, but it is not a poikilotherm in the same sense that a fish is a poikilotherm.

The terms **ectotherm** and **endotherm** are perhaps the most useful for describing the thermal capabilities of animals because they have a mechanistic basis. An ectotherm is an animal whose thermal balance is predominated by external sources of heat, and its metabolic heat production is insignificant. Ectotherms that absorb heat by basking in sunlight are called **heliotherms**, whereas ectotherms that absorb heat from the substrate are called **thigmotherms**. Essentially all animals, except birds, mammals, and a number of insects (and a very few reptiles and fishes), are ectothermic. Endotherms are animals whose thermal balance is predominated by their endogenous metabolic heat production. Adult birds, mammals, and a number of insects (and a very few reptiles and fish) are endothermic. Some endotherms temporarily become ectothermic when cold stressed or deprived of food or water; they are called **heterotherms**. Endothermy is not synonymous with thermoregulation and ectothermy is not synonymous with thermoconformation. In general, endotherms thermoregulate and thermoconformers are ectothermic, but many ectotherms thermoregulate (see Table 5–2).

The distinction between ectotherm and endotherm is not absolute and clear cut. All ectotherms have some metabolic heat production but their $T_b - T_a$ differential is generally negligible, whereas endotherms can sustain much larger $T_b - T_a$ differentials, e.g., 40° C or more. However, some large and active ectotherms have a sufficiently high metabolic production and low heat loss that their metabolic $T_b - T_a$ differential is significant, although still generally small, i.e., 3 to 10° C. Furthermore, endothermy evolved from ectothermy and so there must have been a gradual transition from ectotherm to endotherm. It is difficult to define the specific point at which these transitional animals would cease being ectothermic and become endothermic. Nevertheless, the concepts of ectotherm and endo-

TABLE 5–2

General thermal classification of major groups of animals based on whether they thermoconform/thermoregulate and are ectotherms/endotherms.		
Thermoconform	Many aquatic invertebrates Most terrestrial invertebrates Most fish Most amphibians, some reptiles	Ectotherm
Thermoregulate	Some aquatic vertebrates Some terrestrial invertebrates Some fish A few amphibians, many reptiles Some large, active fish (tuna, sharks) Many insects Some brooding female pythons Birds and mammals Mammals	Endotherm

therm provide a mechanistic and relatively objective definition for distinguishing between two fundamentally different thermal strategies.

The terms **eurythermal** and **stenothermal** define the range of thermal tolerance. An animal that tolerates or is active over only a narrow range of T_b is a stenotherm. For example, many mammals and birds are stenothermic; they cannot tolerate a change in T_b by more than a few degrees. Some lizards, such as the desert iguana, are stenothermic thermoregulators; they regulate T_b within a narrow range (e.g., 37° to 39° C) while active. The alligator lizard, in contrast, is eurythermal; it is active over a wide range of T_b.

Let us examine the mechanisms for heat exchange, the various thermal strategies of ectothermy/endothermy and thermoconformation/thermoregulation, the physiological consequences of these patterns, and the biochemical and physiological adaptations of animals to their thermal environment.

Heat Exchange

The heat exchange between two inanimate objects is proportional to the difference in their temperatures. Furthermore, animals continually produce metabolic heat (Chapter 4), which must be dissipated to the environment. Animals also evaporate water and this can significantly influence their thermal balance.

Animals cannot avoid heat exchange between their body tissues and the environment, but they can manipulate the various avenues of heat exchange to

their thermal and physiological advantage. It is therefore important to understand the basic mechanisms for the three main avenues of heat exchange: **conduction, convection, and radiation.** We must also consider a change in state of water (i.e., **evaporation/condensation** and **freezing/melting**) as an additional avenue for heat exchange.

Conduction

The direct transfer of heat between two solid materials in physical contact is **conduction.** Heat flows from a region of high temperature to a region of lower temperature. The heat transfer occurs on an atomic scale as the exchange of kinetic energy between adjacent molecules. The rate of exchange (flux) by conduction between two objects depends on their area of physical contact, the difference in their temperatures, and their thermal conductive properties.

Fourier's law of heat transfer (for 1-dimensional heat exchange) summarizes the determinants of conductive heat flow

$$Q_{cond} = -kA(T_2 - T_1)/x = C\Delta T \qquad (5.5a)$$

where Q_{cond} is the rate of heat exchange (J sec^{-1}), k is the thermal conductivity (J sec^{-1} °C^{-1} cm^{-1}), A is the contact area for conduction (cm^2), ΔT is the temperature difference (°C), and x is the distance between the two temperatures (cm). The negative sign indicates that heat flow occurs from the highest temperature to the lowest temperature. The **temperature gradient** is the difference in temperature per unit distance for conduction, i.e., $(T_2 - T_1)/x$. The

thermal conductance (C; J sec^{-1} °C^{-1} or various other units) is often used instead of ($-kA/x$) because A and x are often difficult to measure. It is also called a conductive heat transfer coefficient ch$_{cond}$.

Fourier's law for heat transfer by conduction is equivalent in form to Fick's first law for 1-dimensional exchange of material by diffusion (Chapter 3); the thermal conductivity (k) is equivalent to the diffusion coefficient (D) and the temperature difference (ΔT) to the concentration difference (ΔC). Heat conduction can be considered to be thermal energy diffusion from a "high concentration" of heat to a "lower concentration" of heat. Heat conduction can also be considered to be propagation of heat waves (like photons of light) rather than diffusion, and heat waves have been experimentally verified in low temperature liquids and crystals (Maddox 1989). Fortunately, Fourier's law remains valid for most practical purposes.

Thermal conductivity (k) is a material property; it varies dramatically for different materials from $2.4 \ 10^{-2}$ for still air to >100 J sec^{-1} °C^{-1} m^{-1} for metals (Table 5–3). The **insulation** is the reciprocal of the total heat flux per m² of surface area per °C temperature difference. The SI unit for insulation is °C m² sec J^{-1}. The industrial unit for insulation is the clo ("clothing unit"); 1 clo = 0.155 °C m² sec J^{-1}.

The **resistance** of an insulative layer (r; sec cm^{-1}) to heat flux indicates both the thermal conductivity property of the layer and its thickness

$$Q_{cond} = \rho C_p A \Delta T/r \qquad (5.5b)$$

where ρC_p is the volumetric specific heat capacity of the medium (air; 1200 J m^{-3} °C^{-1}; Walsberg, Campbell, and King 1978). There is an inverse relationship between thermal resistance and thermal conductivity.

$$r = \rho C_p l/k \qquad (5.5c)$$

Values for r per meter (i.e., sec m^{-2}; Table 5–3) are essentially the reciprocal of thermal conductivity and are analagous to the inverse of a diffusion coefficient (D; m² sec^{-1}). Most animal and synthetic insulation has an insulative value/thermal conductivity similar to that of air. Indeed, it is the still air trapped within insulative materials that provides their low conductivity. The insulative value of a material increases with resistance and thickness. The insulative value of fur (or feathers) and thermal resistance increases with the thickness of the fur layer (Figure 5–5). Shrew fur (<0.5 cm thick) has a lower insulation than polar bear fur (6 cm thick). However, the insulation per thickness is lower for

thicker fur; shrew fur has a higher insulation per thickness than polar bear fur. Fur or feathers immersed in water have a lower insulative value than in air because (1) water has a higher specific heat and thermal conductivity, (2) they are compressed by the water and have a lower thickness, and (3) they cannot be pilo-erected (fur) or ptilo-erected (feathers). For example, the insulation of eider duck feathers is about 1.62 °C m^{-2} sec J^{-1} in air. The insulation of peripheral tissues contributes a further 0.20 °C m^{-2} sec J^{-1}, and so the total insulation is 1.82 (Jenssen, Ekker, and Bech 1989). The insulation is reduced in water by about 1/2 (to 0.83) for feathers but increased for tissues (0.35); the total insulation is lower in water (1.18) than in air (1.82).

TABLE 5–3

Thermal conductivity (k), resistance (r) to heat loss per meter, and insulation (Clo) per meter, for air, a variety of animal insulation materials (fur, feathers), and other materials.

Material	Thermal Conductivity (J sec^{-1} m^{-1} °C^{-1})	Resistance/m[a] r m^{-1} (sec m^{-2})	Insulation/m[b] Clo m^{-1} (°C m sec J^{-1})
Vaccuum	0	∞	∞
Still air	2.4 10^{-2}	5.0 10^4	269
Red fox fur	3.6 10^{-2}	3.3 10^4	179
Lynx fur	3.8 10^{-2}	3.2 10^4	170
Husky dog fur	4.1 10^{-2}	2.9 10^4	157
80/20 Goose down	5.3 10^{-2}	2.3 10^4	122
Polyolefin	5.7 10^{-2}	2.1 10^4	113
Sheep wool	6.3 10^{-2}	1.9 10^4	102
Dacron II	6.5 10^{-2}	1.8 10^4	99
Pigeon feathers (flat)	6.5 10^{-2}	1.8 10^4	99
Wood	1.3 10^{-1}	9.2 10^3	50
Galloway cattle	1.3 10^{-1}	9.2 10^3	50
Helium	1.4 10^{-1}	8.6 10^3	46
Pigeon feathers (erect)	1.6 10^{-1}	7.5 10^3	40
Fat	1.7 10^{-1}	7.1 10^4	38
Rubber	1.7 10^{-1}	7.1 10^3	38
Dry soil	3.3 10^{-1}	3.6 10^3	20
Human tissue	4.6 10^{-1}	2.6 10^3	14
Water	5.9 10^{-1}	2.0 10^3	11
Glass	1.0	1.2 10^3	6.5
Ice	2.2	5.5 10^2	2.9
Steel	46	26	1.4 10^{-1}
Aluminum	240	5	2.7 10^{-2}
Silver	430	2.8	1.5 10^{-2}

[a] r m^{-1} = 1200/k.

[b] Clo m^{-1} = 6.45/k.

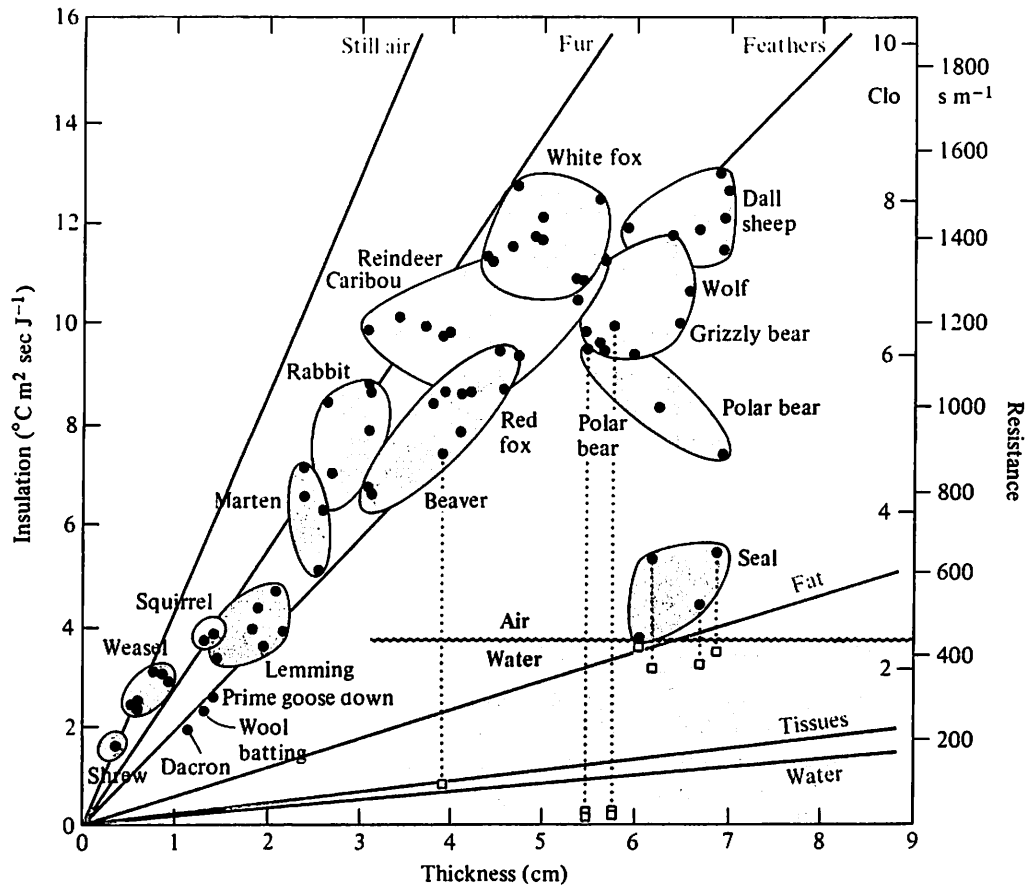**FIGURE 5-5**   The insulative value (°C m² sec J⁻¹) of animal fur varies with its thickness. Fur has a markedly reduced insulative value in water (dotted lines; squares). Seal skin has a low insulative value in air compared to fur but retains most of its insulative value in water. Solid lines indicate the expected values for still air, average values for fur and feathers, fat, tissues, and still water; the slopes of these lines equal 1/thermal conductivity. Solid points indicate some insulative values for artificial insulation (prime 80/20 goose down, wool fiber batting, and Dacron). The alternative insulation scales of resistance (r; sec m⁻¹) and Clo (1 Clo = 0.155 °C m² sec J⁻¹) are also indicated.   *(Modified from Scholander et al. 1950; artificial insulation values from Kaufman, Bothe, and Meyer 1982.)*

Convection

The transfer of heat by the movement of a fluid (liquid or gas) is **convection**. Convective heat exchange is essentially conductive heat exchange across the fluid **boundary layer** (δ), which is the layer of air surrounding the object that varies in temperature from that of the object to that of the free-stream air (see Supplement 5-1, page 187)

$$Q_{conv} = -kA(T_b - T_a)/\delta$$
$$= h_{conv}(T_b - T_a)$$
(5.6)

where h_{conv} is a convective heat transfer coefficient. The value of h_{conv} depends on many complex factors

and should be empirically determined. However, it can be estimated at varying wind velocity from tabulated values for objects of various shapes and sizes.

Convection is **forced** if the fluid movement is produced by an external force (e.g., gravity or a pump). **Free** convection occurs in the absence of forced fluid movement. Fluid near a hot object will be warmer and have a lower density than free-stream fluid; hence, it will rise up from the object. For example, there is a mass flow of air from a naked human in still air of up to 600 liters min⁻¹; the hot plume of air may extend for 1.5 m above the head, and have a velocity of 0.5 m sec⁻¹ (Clark

and Toy 1975). Air near a cold object will cool, have a higher density, and flow down from the object.

The importance of free convection depends on the temperature difference between the object and fluid $(T_b - T_a)$, the dimension of the object (x), the fluid's coefficient of thermal expansion $(a = 1/273$ for an ideal gas), and the kinematic viscosity (v).

Radiation

All objects with a surface temperature greater than $0°$ K emit light of specific wavelengths that depends on the surface temperature. The predominant wavelength $(\lambda_{max}$; nm) is inversely proportional to the surface temperature (Wien's law).

$$\lambda_{max} = 2.898 \; 10^6/T \qquad (5.7)$$

The spectral emission has a λ_{max} of 500 nm for the sun (surface temperature $= 5800°$ K), 1999 nm for an incandescent lamp (2900° K), and 9722 nm for an object at room temperature (293° K). Animals emit long wavelength infrared radiation (IR) because their surface temperature is low. A thermogram measures the emitted IR radiation and represents it as visible wavelengths. The thermograms of a mouse and a lizard, for example, show the variation in surface temperature (Figure 5–6). The energy of the emitted light (kJ mole photons^{-1}) can be calculated from wavelength (nm) as $119660/\lambda$.

The total rate at which an object emits radiant energy is proportional to the fourth power of its surface temperature T_s (Stefan's law)

$$Q_{rad} = \sigma \epsilon A T_s^4 \qquad (5.8a)$$

where σ is the Stefan-Boltzmann constant, ϵ is the emissivity (dimensionless), and A is the radiative surface area (m^2). An ideal radiator (a "black body") has $\epsilon = 1$; most biological materials have an ϵ of 0.90 to 0.95. Objects at temperatures in the biological range emit relatively little energy (300 to 500 J sec^{-1} m^{-2}) compared to very hot objects such as the sun (6.1 10^7 J sec^{-1} m^{-2}). However, 300 to 500 J sec^{-1} m^{-2} is a lot of energy, compared to the metabolic rate of animals. For example, a mammal with a fur surface area of 1 m^2 would emit about 480 J sec^{-1} (if surface temperature was 35° C); the basal metabolic rate would be about 20 J sec^{-1} (if it weighed 10 kg) and the free convective heat loss would be about 20 J sec^{-1} (if $T_b - T_a$ was 10° C and the fur was 2 cm thick).

Animals not only emit radiation but also receive radiation from their environment, i.e., they have a net radiative heat exchange. The net radiative heat exchange between an animal and its environment can be quite complex. Consider first the simple example of an object surrounded by a large surface, and separated from it only by a gas (which has no effect on radiative heat transfer). The **net radiative heat exchange** is
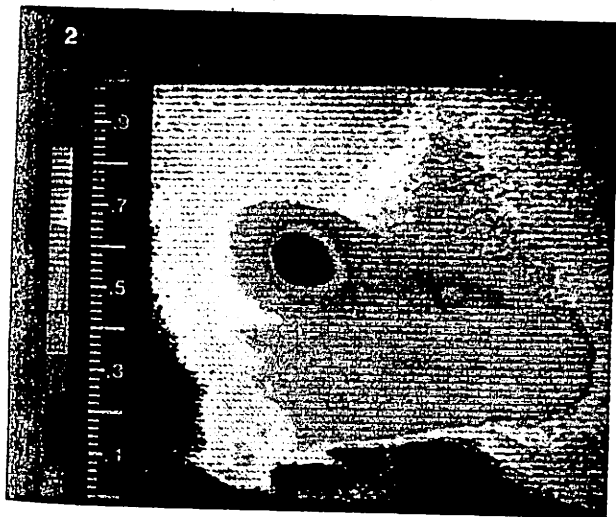
LIZARD
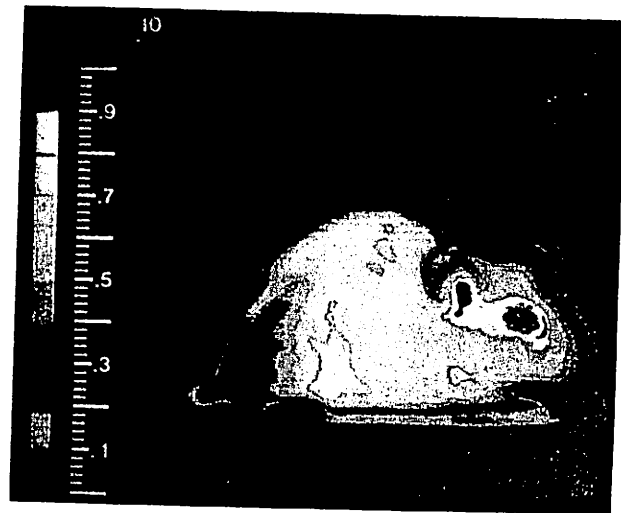
MOUSE

FIGURE 5–6 Thermogram of a mouse (right) and the head of a monitor lizard (*Varanus salvator*; left) showing the variation in surface temperature. The color corresponds to the elevation of surface temperature above background (about 25° C); the scale for the lizard corresponds to a temperature difference of 2° C, whereas the scale for the mouse is 10° C. *(From den Bosch 1983.)*

$$Q_{\text{rad,net}} = \sigma \epsilon A (T_s^4 - T_{\text{sur}}^4) \qquad (5.8b)$$

where T_{sur} is the temperature of the surrounding surface. If T_s is approximately equal to T_{sur}, then there is little net radiative heat exchange because the object gains an equivalent amount of radiative heat from its environment.

The equation for $Q_{\text{rad,net}}$ is of a different form from those for conduction and convection, where Q was proportional to $(T_b - T_a)$. However, it can be converted to a similar form by defining a radiative heat transfer coefficient (h_{rad}) so that

$$Q_{\text{rad,net}} = h_{\text{rad}}(T_s - T_{\text{sur}}) \qquad (5.8c)$$

However, we must appreciate that h_{rad} depends markedly on both T_s and T_{sur} because

$$h_{\text{rad}} = \sigma \epsilon (T_s + T_{\text{sur}})(T_s^2 + T_{\text{sur}}^2) \qquad (5.8d)$$

In contrast, h_{cond} is independent of temperature, and h_{conv} is only weakly dependent on temperature.

Evaporation/Condensation

Evaporation of water dissipates considerable heat. The latent heat of evaporation is 2500 J g^{-1} at 0° C, 2400 at 40° C, and 2260 at 100° C. This is much more energy than is required to melt ice (latent heat of fusion is 334 J g^{-1}) or to heat water from 0 to 100° C (about 418 J g^{-1}).

The evaporation of water depends not on the temperature difference between the animal and its environment, but on (1) the difference in water vapor density between the animal and the ambient air, and (2) the resistance to water loss from the surface

$$Q_{\text{evap}} = \frac{DA(\chi_b - \chi_a)}{x} = \frac{A(\chi_b - \chi_a)}{r}, \qquad (5.9)$$

where D is the diffusion coefficient for water vapor, A is the area, χ is the absolute water vapor density (g m^{-3}), x is the pathlength for water loss, and r is the resistance to water loss. We generally assume that the air at the animals' surface is saturated (100% RH) at the surface temperature. Consequently, χ_b depends on surface temperature, and is proportional to body temperature.

Condensation occurs if $\chi_b < \chi_a$, and heat is gained rather than lost.

Heat Balance

The thermal balance of an animal is determined by the net exchange of heat by all of the avenues for heat exchange that we have discussed, as well as

by metabolic heat production. Animals must, in general, be in heat balance, i.e., heat gain = heat loss. Otherwise, body temperature would decrease (heat gain < heat loss) or increase (heat gain > heat loss). However, an animal can be in transient positive or negative heat balance and changes in body temperature can buffer the thermal imbalance.

The general equation describing heat balance is

$$\begin{aligned} M = \; & h_{\text{cond}}(T_b - T_a) \\ & + h_{\text{conv}}(T_s - T_a) \\ & + h_{\text{rad}}(T_s - T_{\text{sur}}) \qquad (5.10a) \\ & \pm E \\ & \pm S \end{aligned}$$

where M is metabolic heat production, E is evaporative/condensative heat transfer, and S is storage or loss of heat by a change in body tissue temperature. The various heat transfer coefficients (h_{cond}, h_{conv}, h_{rad}) vary markedly depending on the specific circumstances, but approximate ranges of values indicate that conduction, free convection, and radiation have similar h values, forced convection in gases has a higher h, forced convection in liquids has an even higher h, and forced convection with evaporation can have extremely high h values (Table 5–4).

The general equation for heat balance can be greatly simplified for steady-state ($S = 0$) if T_s is approximately equal to T_{sur} and we ignore condensation

$$M - E = h(T_b - T_a) \qquad (5.10b)$$

where h is the total nonevaporative heat transfer coefficient.

TABLE 5–4

Typical values for heat transfer coefficients by conduction, free or forced convection, convection with evaporation, and radiation.	
	h (J sec^{-1} m^{-2} °K^{-1})
Conduction	
Air	0.5–5000
Water	50–5000
Convection	
Free	2–25
Forced—air, dry	25–250
Air, with evaporation	2500–100000
Water	50–20000
Radiation (excluding direct solar)[1]	4–8

[1] Solar radiation heat gain can be about 200—1000 J sec^{-1} m^{-2} depending on atmospheric conditions and latitude/altitude (the solar constant is 1353 J sec^{-1} m^{-2}).

Ectotherms

The metabolic heat production of ectotherms is generally negligible and their heat balance equation (see Equation 5.10a) reduces to

$$0 = h_{cond}(T_b - T_a) + h_{conv}(T_b - T_a)$$
$$+ h_{rad}(T_b - T_{sur}) \pm E \pm S \qquad (5.11a)$$

One solution to this equation is $T_b = T_a$ if E and S are negligible and $T_{sur} = T_a$, i.e., the animal thermoconforms. However, there are other solutions. For example, a high radiative heat gain ($T_{sur} > T_a$) can significantly elevate T_b above T_a until the heat loss by conduction, convection, and evaporation balances the radiative heat gain.

Let us first examine the thermal relations of aquatic ectotherms that generally do not experience a significant radiative heat load and, therefore, thermoconform, and then let us examine terrestrial ectotherms that often experience a significant radiative heat load and thermoregulate.

Aquatic Ectotherms

The thermal relationships of aquatic ectotherms are constrained not only by their insignificant metabolic heat production, but also by the high thermal conductivity and specific heat of water, by the relative insignificance of thermal radiative heat gain, and by their inability to dissipate heat by evaporation. Water has a much higher thermal conductivity than air, and the specific heat of water and animal and plant tissues is also considerably greater than that of air and other gases, especially on the basis of J liter^{-1} °C^{-1} (Table 5–5).

TABLE 5–5

Specific heat (J g^{-1}°C^{-1} and J liter^{-1} °C^{-1}) for selected materials. *(Modified from Serway 1983; Incropera and Dewitt 1981.)*			
	Density (kg m^{-3})	**Specific Heat**	
		J g^{-1} °C^{-1}	**J liter^{-1}°C^{-1}**
Helium	0.18	5.19	0.93
Water vapor	0.59	1.97	1.46
Air	1.29	1.006	1.2
Oxygen	1.43	0.92	1.22
Carbon dioxide	1.90	0.83	1.63
Cotton	80	1.30	104
Water	1000	4.186	4186
Tissues	1000	3.9	3900
Clay	1460	0.88	1285
Gold	19300	0.13	2509

Heat dissipation across gills is so effective for most aquatic animals that metabolic heat production has no thermal significance and T_b is similar to T_{water}. Metabolic heat production has no thermal consequences for aquatic ectotherms because the heat dissipation capacity of gill ventilation of water far exceeds the capacity for metabolic heat production. The temperature differential between the body and water (ΔT) can be calculated from the oxygen solubility coefficient for water (α_{O_2}; 0.0115 μM L^{-1} Pa^{-1} for seawater at 20° C), the ambient O_2 partial pressure (pO$_2$; 21200 Pa), and percentage O_2 extraction from the water (E$_{O_2}$; often about 50%) as 1.08 10^{-6} O_2 pO$_2$ E$_{O_2}$. The ΔT is less than 0.03° C even if the α_{O_2} extraction is 100%. In contrast, the ventilatory heat loss of an air-breathing animal due to the warming of the respiratory air flow is 0.00154 pO$_2$ E$_{O_2}$. The ΔT in air is about 163° C for a typical O_2 extraction of 5% and is over 3000° C for 100% extraction!

Aquatic ectotherms thus have thermal constraints that generally preclude significant elevation of T_b above T_{water}. Consequently, the heat exchange equation for aquatic ectotherms reduces to the simple form of

$$0 = h_{cond}(T_b - T_{water}) + h_{conv}(T_b - T_{water}) \quad (5.11b)$$

and so $T_b = T_{water}$ since the thermal gradient is the same for both conductive and convective heat exchange (an aquatic animal cannot gain heat by conduction but at the same time lose heat by convection). For example, the body temperature of aquatic ectotherms is generally not very different from water or substrate temperature (Figure 5–7A). However, some large fish can selectively warm certain tissues and restrict heat flow to the gills, and some large air-breathing sea turtles can have T_b substantially higher than T_{water}.

Many aquatic ectotherms are able to precisely thermoregulate at a **preferred body temperature** ($T_{b,pref}$). The thermal preferences for a number of fish and other aquatic ectotherms are summarized in Table 5–6. This regulation of $T_{b,pref}$ is accomplished by behavioral selection of a suitable water temperature, rather than thermoregulation by physiological means. Many fish maintain body temperature in a narrow range if there is a suitable gradient in water temperature. For example, bluegill sunfish select a T_b of about 26° C in a thermal gradient providing a range of T_{water} from 6° to 34° C (Figure 5–7B).

Amphibians are a particularly interesting group of ectotherms because many species are transitional between aquatic and terrestrial environments. They
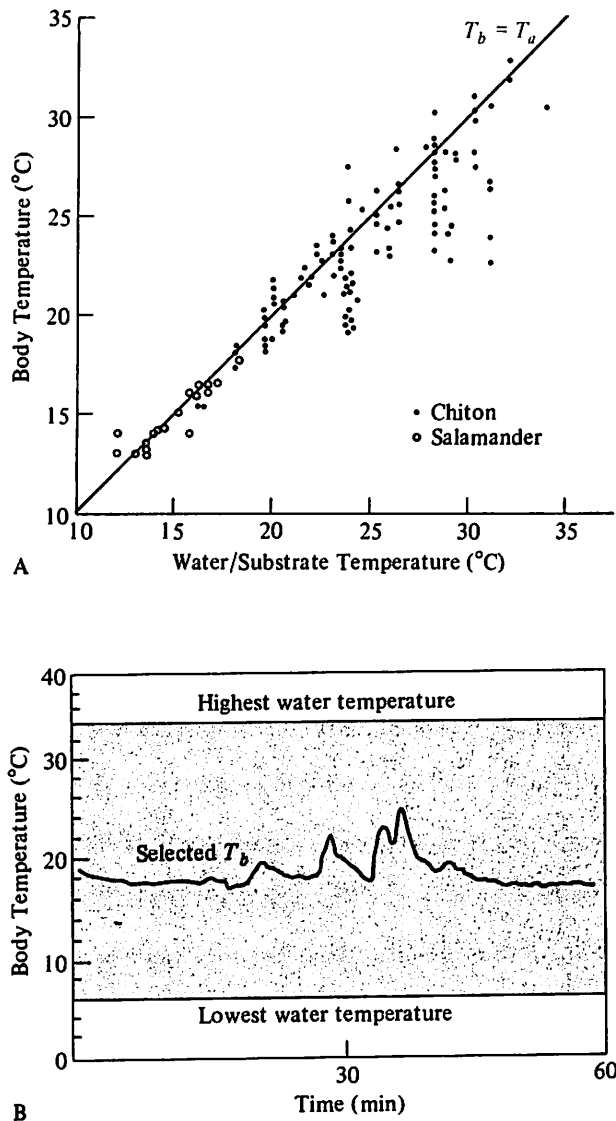
TABLE 5-6

Preferred body temperatures (°C) for some invertebrate and lower vertebrate ectotherms.	
Arthropods	
Wireworm	17
Blowfly	20–25
Flour beetle	25–30
Earwig	25–30
Louse	29–30
Leather beetle	30
Housefly larva	30–37
Chicken louse	42.5
Fish	
Largemouth bass	24
Opal-eye shorefish	26
Bluegill sunfish	26
Brown bullhead	26
Carp	22–28
Amphibians	
Salamander tadpoles	25
Grass frog tadpoles	23–30
Bullfrog tadpoles	24–30
Bullfrogs	22–28
Gray treefrog	up to 38
Phyllomedusa	up to 40
Aquatic Reptiles	
Box turtle	21–25
Painted turtle	29–35
Alligator	32–35

FIGURE 5-7 (A)   Relationship between body temperature (T_b) and water temperature (T_w) for an aquatic salamander *Taricha torosa*, and between T_b and substrate temperature (T_{sub}) for a chiton *Clavarizona hirtosa*.
(B) Continuous recording of body temperature (dorsal muscle) of a bluegill sunfish in a thermal gradient (6° to 36° C temperature range).   *(From Brattstrom 1963; Kenney 1958; modified from Crawshaw 1975.)*

have T_b's from about 0° C (e.g., a salamander walking over a snow field) to over 40° C (a basking "waterproof" frog). As we would expect, aquatic amphibians have a T_b similar to T_{water}, but many select a preferred T_b if there is a suitable thermal gradient in T_{water}. For example, many tadpoles select the warmer water around the edges of a pond and avoid the cooler, deeper water (Brattstrom 1970). *Hyla regilla* tadpoles orient so that their dorsal surface is exposed to solar radiation. Aggregations of tadpoles can absorb sufficient solar radiation to increase the local T_{water} (Brattstrom 1962). Tadpoles also select a preferred range of T_b in a thermal gradient (Table 5–6).

Terrestrial amphibians have the potential to raise T_b by choosing suitable microclimates or by basking in sunlight, but their high cutaneous evaporative loss tends to decrease the efficiency of heliothermic basking. It has been suggested that basking is thermally ineffective and behavioral thermoregulation would be crude, at best, for amphibians because their evaporative water loss would dissipate essentially all of the solar heat gain (Tracy 1976). Nevertheless, many terrestrial amphibians behaviorally thermoregulate by choosing thermally-favorable microclimates and by basking in the sun. For example, juvenile green toads (*Bufo debilis*) basking in the sun have a T_b 10° to 15° C above that of animals in the shade. Juvenile bullfrogs (*Rana catesbeiana*) select a T_b of 27° to 28° C in a thermal gradient and bullfrogs in the field have a T_b of about 30° C. These patterns of thermoregulation are, however,

relatively crude compared to the thermoregulatory capacity of many other terrestrial invertebrates and vertebrates (see below).

Terrestrial Ectotherms

Many terrestrial ectotherms have a considerable capacity for behavioral and physiological thermoregulation. Air has a lower thermal conductivity and heat capacity than water, so it is easier for terrestrial ectotherms to maintain a thermal gradient between T_b and T_a, and T_b will equilibrate more slowly with T_a. The rate of cooling (or warming) of an object, or animal, in a cooler (or warmer) environment is determined by the temperature differential, the

surface properties (i.e., surface area and nature of insulation) and the thermal properties of the medium (i.e., conductivity and specific heat).

The rate of change in T_b is proportional to $(T_b - T_a)$ and decreases as T_b approaches T_a. The T_b changes in an exponential fashion (Figure 5–8A) towards an equilibrium temperature (that is close to, but not necessarily equal to, the ambient temperature). The general equation for conductive or convective heat loss is

$$Q = h(T_b - T_a) = C_p M\delta(T_b - T_a)/\delta t \quad (5.12a)$$

where C_p is the specific heat (J g^{-1}), M is mass (g), and $\delta(T_b - T_a)/\delta t$ is the rate of change in $(T_b - T_a)$
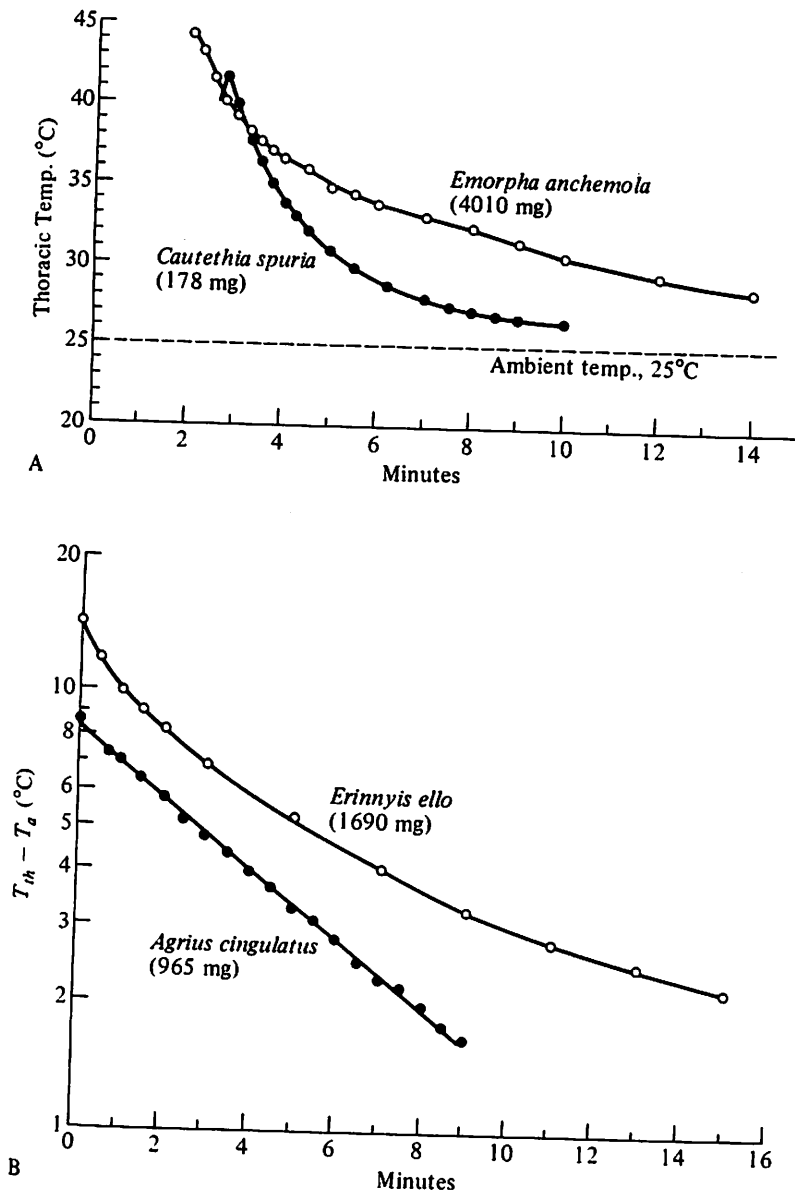

FIGURE 5–8 (A) Time course for thoracic cooling of the sphinx moths *Emorpha* and *Cautethia*. (B) Semilogarithmic plot of cooling curves for the sphinx moths *Erinnyis* and *Agrius*; the initial steep part of the cooling curve for *Erinnyis* indicates facilitated heat loss. *(From Bartholomew and Epting 1975.)*

over time (t). This equation can be rearranged and integrated to yield

$$\ln (T_b - T_a) = \frac{h}{C_p M}t + \text{con}$$

$$= CCt + \text{con}$$ (5.12b)

where t is time (min) and con is a constant of integration. Consequently, the exponential change in T_b over time for a cooling or warming curve can be linearized (Figure 5–8B) by graphing $\ln (T_b - T_a)$ against time (Morrison and Tietz 1957). The slope of this line ($h/C_p M$) is called the cooling constant (CC; h^{-1}). The cooling constant is converted to a thermal conductance (C; $J\,g^{-1}\,h^{-1}\,°C^{-1}$) by accounting for the specific heat of tissues (C_p; generally about 3.4 $J\,g^{-1}\,°C^{-1}$); $C = 3.4\,CC$.

Many variables affect the thermal conductance of animals. The most important are body size (hence surface area for heat exchange), presence of insulation, and the nature of the medium (air or water). Body mass is important since the surface area:volume ratio of the animal determines the ratio of heat dissipation capacity:heat content. Large animals have a lower surface area:volume than small animals, and therefore cool (or warm) slower, e.g., the larger (4 g) sphinx moth *Emorpha* cools more slowly than the smaller (0.2 g) sphinx moth *Cautethia* (Figure 5–8A). The scaling of thermal conductance varies for different groups of animals (e.g., insects, lizards, mammals, birds) but there is a general trend that C is proportional to $\text{mass}^{-0.5}$, with an intercept value (i.e., C for a 1 g animal) of about 30 $J\,g^{-1}\,h^{-1}\,°C^{-1}$. For insects, the thoracic mass is often used rather than the body mass because it is primarily the thoracic temperature that is regulated.

The inverse relationship between C and body mass has profound biological significance. Small animals have considerable difficulty in maintaining a temperature differential; for example, a 20 mg bee will cool almost to ambient temperature within a few minutes. In contrast, a large animal has such a low conductance that its T_b is relatively constant. A 2000 kg dinosaur would hardly warm or cool over a 48 h period, by virtue of its gargantuan size. The thermal conductance of such a large animal is also the same in air and water.

Factors other than body size also influence thermal conductance. The intercept value is often higher for live than dead insects, perhaps reflecting the contribution of blood flow in live animals to heat dissipation from the thorax. Dead insects also have a greater mass dependence of thermal conductance than live insects. Conductance is also expected to be marginally higher for dead than for live animals because of metabolic heat production.

Insulation affects thermal conductance. For example, bees with their body hairs removed have a higher conductance than normal bees. However, insulation is often not as important as might be expected (May 1976). For example, tabanid flies have only very short hairs whereas sphinx moths have a very long, dense cover of scales, but their conductances are similar. Species of bees that are virtually hairless have conductance similar to hairy species. This is probably because the boundary layer of air around an insect's body is probably of greater significance than the insulation (at least under the experimental conditions of low convection). The thermal conductance of the insulated insects would be expected to be lower than that of the naked insects at high wind speeds when the boundary layer is less important. For example, the seta of the gypsy moth caterpillar decrease the thermal conductance more at high wind velocity than at lower velocity, or with free convection. The air boundary layer resistance of lizards is approximately independent of the body mass and is relatively less important in determining heating/cooling rates for larger lizards (Bell 1980).

Animals generally heat faster than they cool; this is particularly apparent for lizards and crocodilians. There is also a similar hysteresis in heart rate (faster during heating) and metabolic rate (higher during heating). Cardiovascular and metabolic adjustments presumably facilitate heating and retard cooling. For example, lizards and crocodiles have peripheral vasodilation during heating and vasoconstriction during cooling (Morgareidge and White 1969; Grigg and Alchin 1976). Such cardiovascular adjustment requires an augmented peripheral blood flow that is unrelated to metabolic demand. A right-to-left intracardiac shunt increases the ventricular systemic outflow for the iguana during heating (Baker and White 1970).

The allometry of thermal conductance for most insects, birds, and mammals is similar to that predicted for free convective heat loss in air, i.e., their thermal conductance is near the minimal possible value (Figure 5–9). In contrast, reptiles in water have a higher thermal conductance, close to that predicted for a cylindrical object in water with maximum convective heat loss. Small reptiles in air have an intermediate thermal conductance. Very large reptiles would have a thermal conductance similar to that of large mammals, and the free convective minimal value, whether they are in air or water.
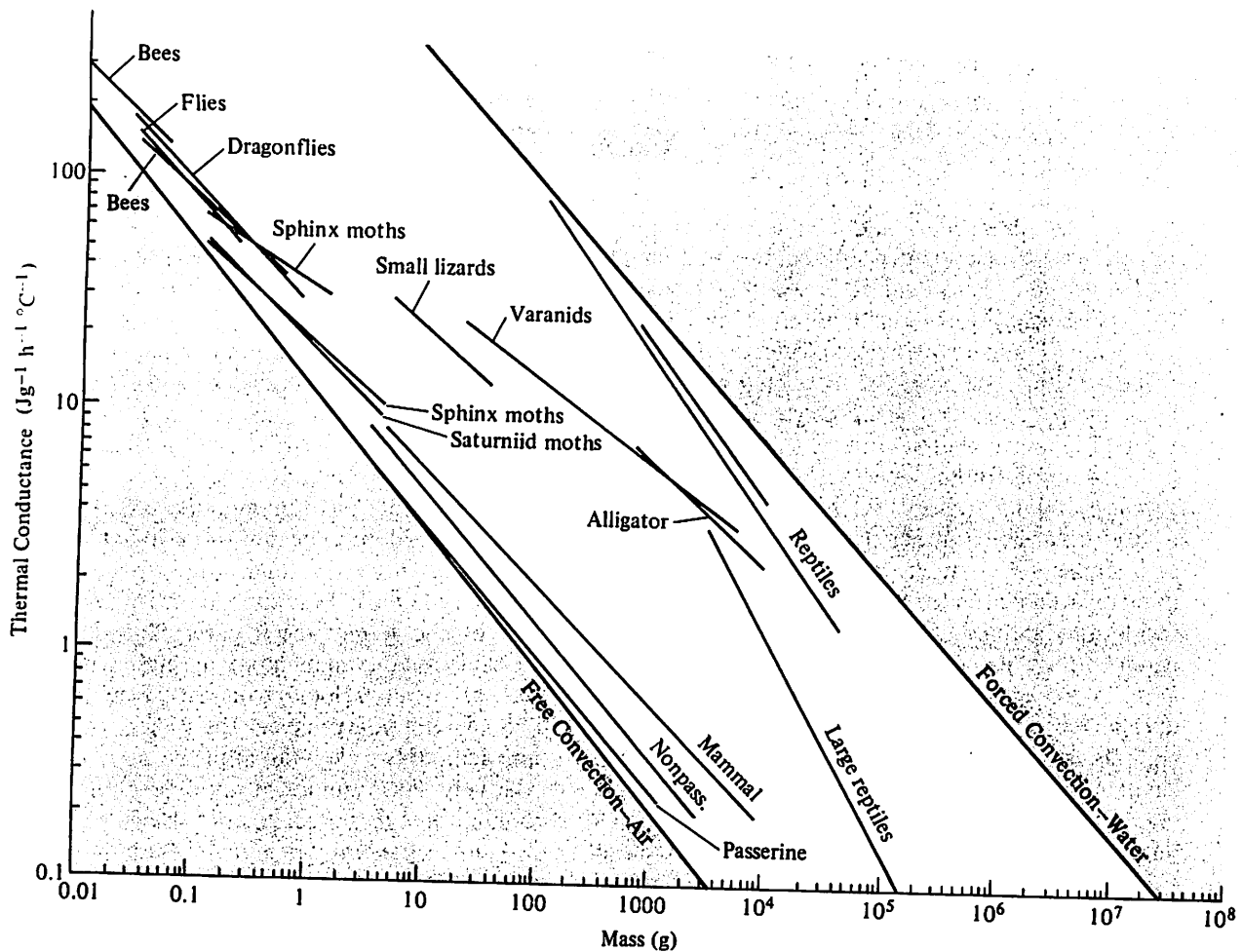
FIGURE 5–9 Allometric relationships for minimal thermal conductance of insects and vertebrates. Thin lines indicate relationships for air; heavy lines indicate relationships for water. Free convection air line indicates the minimal thermal conductance for free convective heat loss from a sphere in still air. Forced convection water line indicates the maximal thermal conductance for forced convective heat loss of a cylinder in water.

The extent to which animals can behaviorally or physiologically thermoregulate is indicated by the relationship between T_b and T_a (Figure 5–10). The slope is 1 for total dependence of T_b on T_a, i.e., thermal conformation, and 0 for thermal independence. The precision of thermoregulation is indicated by the extent of scatter of data points around the regression line.

Basking Insects. Body posture and orientation of the wings can markedly affect the body temperature of basking insects. "Perching" dragonflies bask at low air temperatures and regulate their radiative heat gain by postural adjustment (Figure 5–11A). Several species bask with the wings positioned forward and downward to reduce convective heat loss. Other dragonflies ("fliers") use endogenous heat production for thermoregulation (see Endothermic Insects, page 173). Many butterflies can elevate thoracic temperature by as much as 15° C above T_a by postural adjustment, although some species also use endogenous heat production to elevate T_{th}. Many bask with the wings held to the side of the body and the thorax perpendicular to the sun ("dorsal baskers"), with the wings held vertically over the body and perpendicular to the sun ("lateral baskers"), or with the forewings vertical and the hindwings flattened ("body baskers"). The wing area nearest the body is the most effective in facilitating heat gain by the thorax (Figure 5–11B). Syrphid
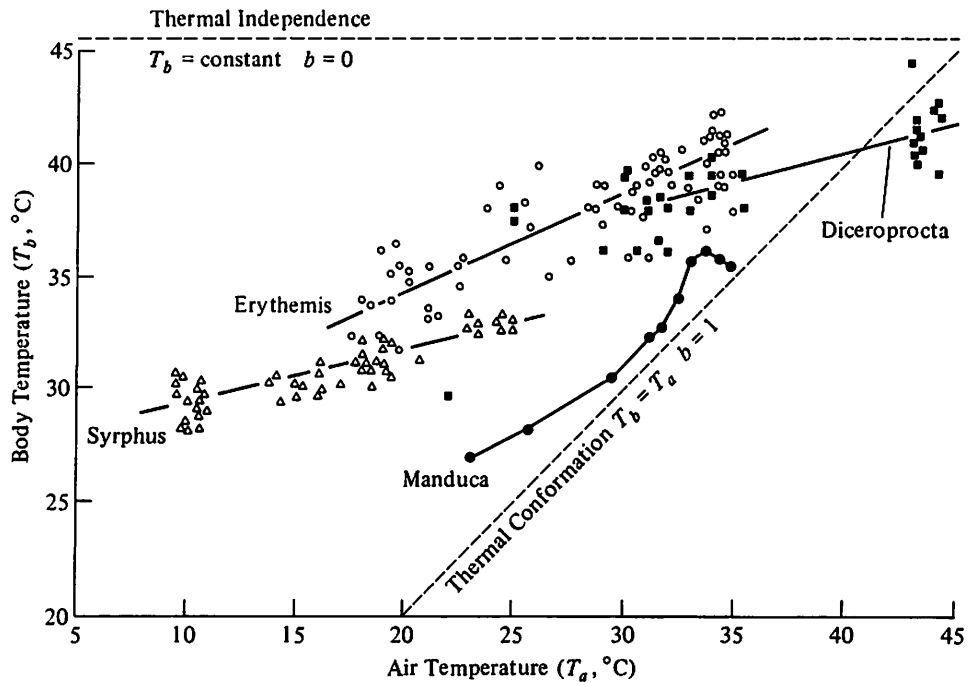
FIGURE 5–10   Thoracic temperature as a function of air temperature in desert cicadas (*Diceroprocta*), hoverflies (*Syrphus*), sphinx moth caterpillars (*Manduca*), and dragonflies (*Erythemis*).

hoverflies use a combination of behavior (perching in sun or shade) and endogenous heat production to thermoregulate. Caterpillars rely on behavioral rather than endogenous mechanisms for thermoregulation. Many tenebrionid beetles thermoregulate behaviorally (although some are endothermic).

Ground-dwelling insects are especially prone to overheating because they are in the boundary layer of the ground surface. They intercept considerable direct and reflected solar radiation, and also infrared radiation, conductive and convective heat from the ground. Consequently, many different types of ground-dwelling arthropods (tenebrionid beetles, locusts, scorpions) raise their bodies as high off the ground as possible ("stilt") to minimize heat gain from the ground, to move the body into the cooler part of the thermal boundary layer, and to increase convective heat loss in the higher velocity part of the velocity boundary layer. For example, the locust *Schistocerca* adopts a crouched posture when the ground is warmer than the air (to warm up) and adopts a semistilted (head off ground) or stilted posture (entire body off ground) when the ground is extremely hot. Locusts and some caterpillars also orient with reference to both the sun and wind, to vary both radiative heat gain and convective heat loss.

Color has significant effects on thermoregulation because about 50% of the radiant energy from the sun is in the visible spectrum. Consequently, the visible reflectance (hence color) influences radiative heat gain. A black surface reflects less radiant energy than a white surface. For example, the Namib desert tenebrionid beetle *Stenocara* has black elytra with a mean reflectance of about 23%, whereas its white sides have a higher mean reflectance of about 35% (Figure 5–12A). Black animals would be expected to absorb more radiation and therefore have a higher T_b than white animals. Tenebrionid beetles (*Onymacris*) with white elytra have a lower T_b than species with black elytra (Figure 5–12B). The black beetles seem to be more active earlier in the day because they absorb more radiation and heat faster, whereas white beetles are more active in the hotter parts of the day because they have less of a radiative heat load. The wing base of some lateral basking butterflies is melanized at the ventral part of the fore and hind wings, and increases the T_b when basking.

Basking Reptiles.   The body temperature of reptiles is quite variable, ranging from only a few degrees to over 40 degrees. Nocturnal and some diurnal lizards thermoconform, with T_b similar to T_a. For
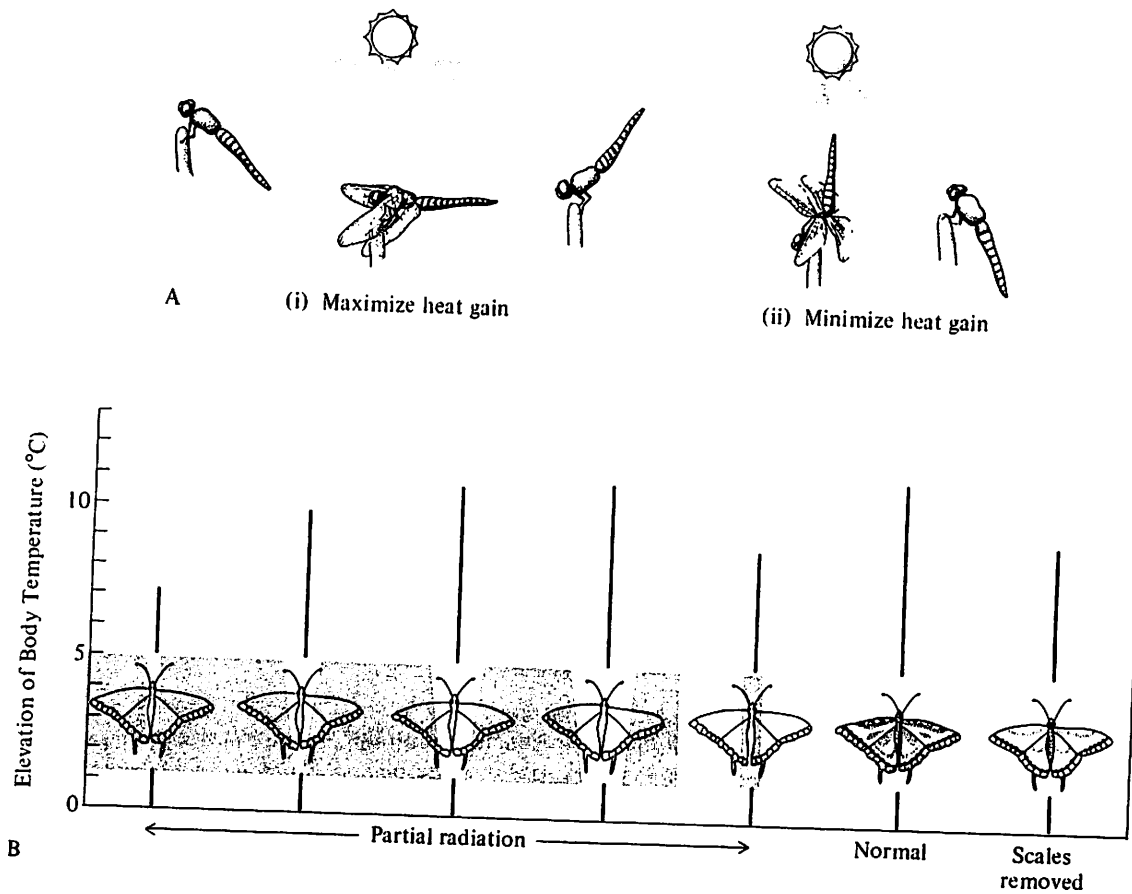
FIGURE 5–11 (A) Postures adopted by a dragonfly to maximize heat gain (i) by heliothermy or (ii) to minimize heat gain. **(B)** Effects of thermal radiation on wings of the butterfly *Papilio* to elevation of thoracic temperature above ambient temperature, and the effects of removing the inner wing scales. *(Modified from May 1976b; Wasserthal 1975.)*
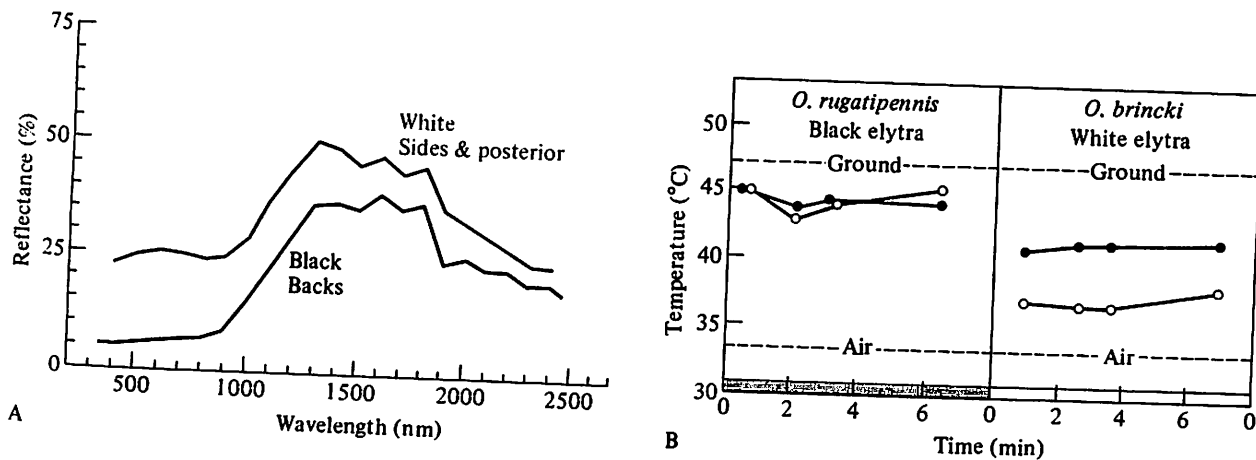

FIGURE 5–12 (A) Reflectance of the black back and whiter side of the Namib desert tenebrionid beetle *Stenocara phalangium*; the mean reflectance is 35% for the whitish side and 23% for the black back. **(B)** Temperature of the thorax (solid symbols) and abdomen (open symbols) of the Namib desert tenebrionid beetles *Onymacris rugatipennis* (black elytra) and *O. brincki* (white elytra) in natural sunlight. *(From Henwood 1975; modified from Edney 1971.)*
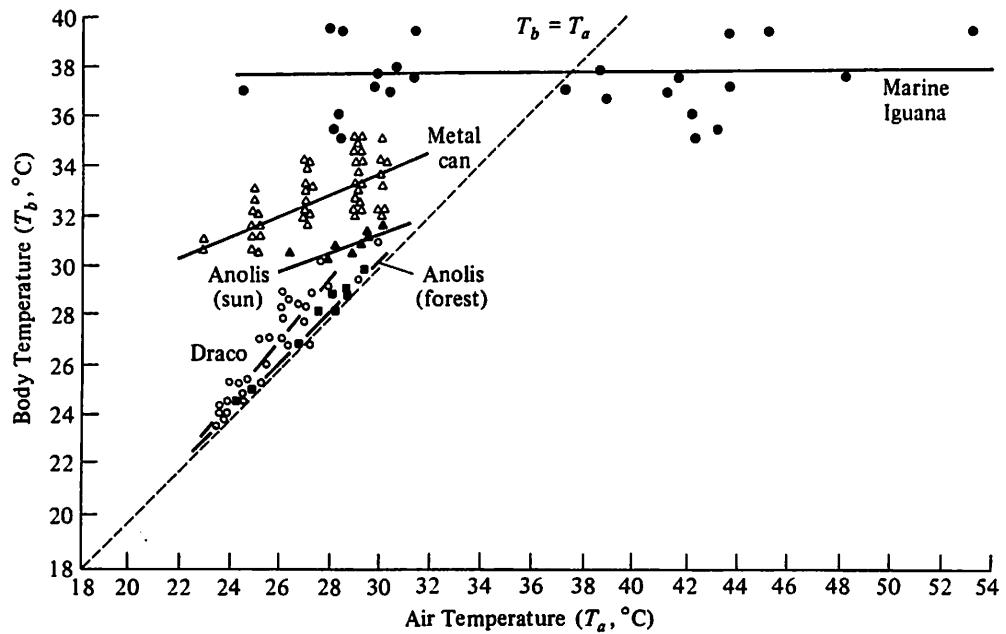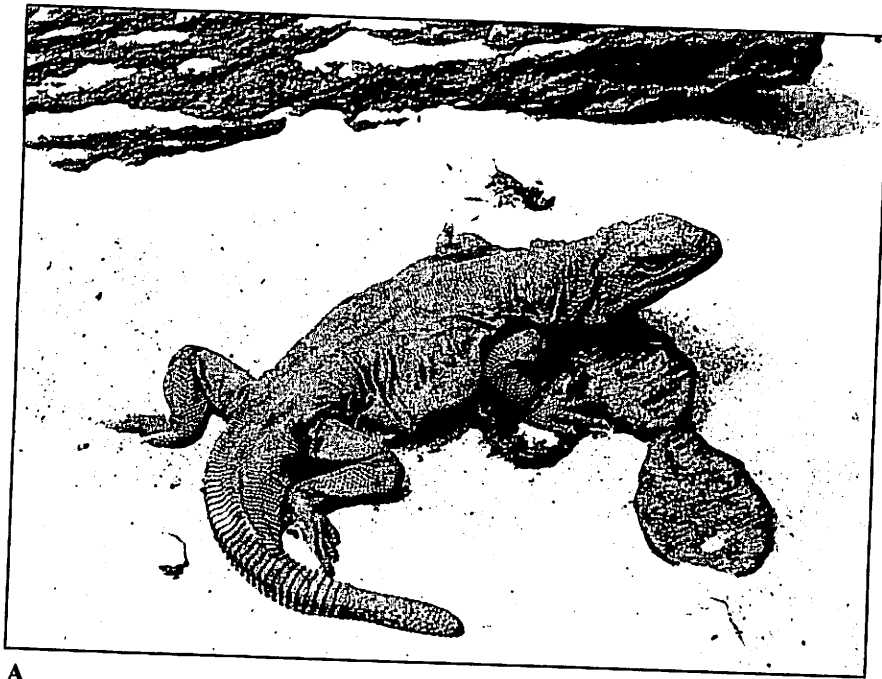
FIGURE 5–13   Relationship between body temperature and air temperature for thermo-conforming lizards (Draco, Anolis, in shaded forest habitat) and thermoregulating lizards (Amblyrhynchus, Anolis, in open habitats); also shown is the relationship for an inanimate object (water-filled metal can).

example, the agamid lizard Draco and the forest Anolis species (Figure 5–13) have T_b similar to T_a. Nocturnal lizards have no solar radiative heat source (although some bask during the day while inactive, e.g., geckos bask under tree bark). Many forest lizards cannot bask because they live in shaded habitats (e.g., some forest floor anoles) or do not bask even if patches of sunlight are available (e.g., the forest floor skink Sphenomorphus). The tropical anole A. cristatellus is a thermal opportunist; it is a thermoconformer in shaded habitats but a thermoregulator in open park habitats (Huey 1974). Some diurnal lizards do not bask because they are active late in the day when the ambient temperature is high enough for normal activity, e.g., the great plains skink Eumeces. Some skinks (Eumeces) and the alligator lizard (Gerrhonotus) absorb heat by ventral contact with a sun-heated substrate or dorsal contact with the undersides of sun-heated rocks. These lizards are thigmotherms because their main heat gain is conductive rather than radiative.

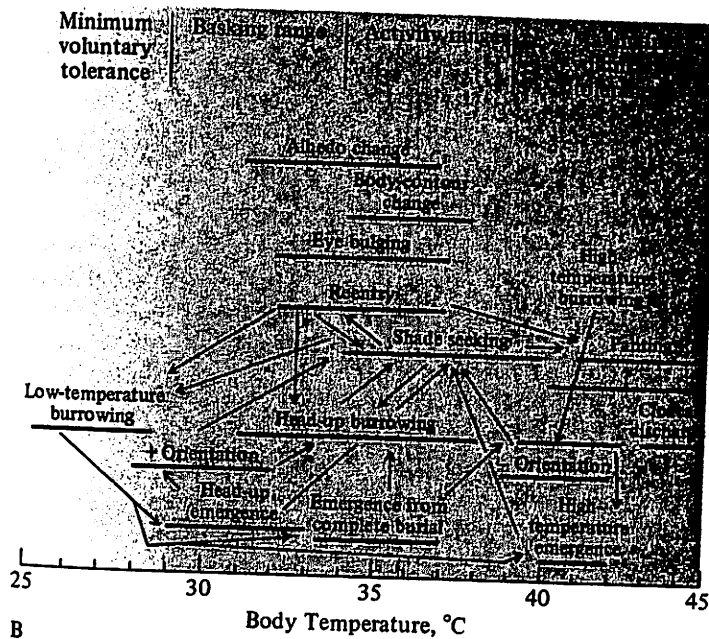Most diurnal lizards bask in sunlight and are accomplished thermoregulators with preferred T_b about 35° to 40° C (e.g., the chuckwalla; Figure 5–14A). These heliothermic lizards manipulate their thermal exchange in a number of behavioral and

physiological ways. These include varying whether they are in sun or shade by movement (shuttling), their orientation to the sun, their skin color, body contour, peripheral vasoconstriction or vasodilation, heart rate, etc. The complex suite of behavioral and physiological mechanisms for heating, regulating T_b, or cooling is well illustrated by the behavioral repertoire of the horned lizard Phrynosoma (Figure 5–14B).

The preferred T_b, or eccritic T_b, is not necessarily the same for lizards in nature as in the laboratory. This reflects the additional complexities of survival in the natural environment, e.g., suboptimal thermal regimens (e.g., cloudy days), and time allocated to activities other than thermoregulation (e.g., feeding, defending territories, finding mates, avoiding predation). There are temporal, physiological, and ecological costs to thermoregulation (Huey and Slatkin 1976; Huey 1982). Thermoregulatory precision is compromised if any, or all, of these costs are substantial. Laboratory experiments have clearly demonstrated a dependence of both the level and precision of T_b regulation on the metabolic cost for thermoregulation. For example, the eurythermal lizard Gerrhonotus can precisely regulate a relatively high T_b of 27.8 ± sd 2.0° C in a low-cost environment, but has a lower T_b and less precision

A

Minimum voluntary tolerance

Low-temperature burrowing

25   30   35   40   45

B   Body Temperature, °C

FIGURE 5–14 (A) A chuckwalla (*Sauromalus*) showing typical heliothermic behavior basking on a rock pile in direct solar radiation. **(B)** The horned lizard (*Phrynosoma*) uses a complex suite of behavioral and physiological responses to thermoregulate. *(Courtesy, Department of Library Sciences, American Museum of Natural History/Raymond L. Ditmars, Neg. no. 16555 and Heath (1965) with permission of the Regents of the University of California.)*

(20.1 ± sd 3.1° C) in a high-cost environment (Campbell 1985). The stenothermic lizard *Dipsosaurus* thermoregulates precisely at a high T_b of 39.1 ± sd 2.0 in a low-cost environment, but has a lower T_b and less precision of 32.9 ± sd 4.0 in a high-cost environment (Withers and Campbell 1985).

Heliothermic lizards balance one set of behaviors and physiology for heat gain against a different set for heat dissipation. Laboratory studies suggest that there are separate thermostats for control of heat gain and heat loss, i.e., there is a dual-setpoint regulatory system (see also Chapter 2). However, the distribution of T_b is not normally distributed about the $T_{b,pref}$, but is **negatively skewed** if the regulatory precision is not the same for the low and high setpoints. For example, the desert iguana *Dipsosaurus* has a modal T_b of about 39° C and a negatively skewed T_b distribution, i.e., there are

more T_b values <39° C than >39° C (Figure 5–15). The lower body temperature setpoint (LBTS) for triggering mechanisms that increase T_b is 36.4 ± sd 1.9° C and the higher body temperature setpoint (HBTS) for mechanisms that lower T_b is 41.7 ± sd 1.3. On average then, the T_b of the lizard will rise to 41.7° C and trigger the heat loss mechanisms (e.g., shuttle into the shade), and T_b will decline until it reaches 36.4° C at which point the mechanisms for heating are triggered (e.g., shuttle into sunlight) and T_b will rise. However, the LBTS and HBTS values of 36.4 and 41.7 are only average values, and the actual minimum and maximum T_b will vary in different thermal cycles. The net effect is that the mean T_b distribution of Dipsosaurus is negatively skewed because the LBTS is more variable than the HBTS. The T_b distribution would be normally distributed if LBTS and HBTS had the same variation, and would be positively skewed if HBTS was more variable than LBTS.

The dual-setpoint model for T_b regulation by heliothermic lizards provides a mechanism to negatively skew the T_b distribution, but what is the physiological significance of a negatively skewed T_b distribution? It is more important to a lizard that T_b not rise above $T_{b,pref}$ and exceed its critical thermal

maximum temperature rather than for T_b to decline below $T_{b,pref}$; consequently, a negatively skewed distribution seems adaptive. Another explanation is that physiological processes typically have a Q_{10} of about 2 to 3. An increase in T_b elevates metabolic rate more than the same decline depresses metabolic rate. For example, if metabolic rate is 1 at 38° C, then a 2° C increase in T_b to 40° C increases VO_2 to 1.20 (a 20% increase) whereas a 2° C decline in T_b to 36° C decreases VO_2 to 0.83 (a 17% decrease), if Q_{10} = 2.5. Consequently, a negatively skewed T_b distribution may result in a normal distribution of the physiological function (such as metabolic rate), whereas a normal T_b distribution would result in a positively skewed distribution of the physiological function (DeWitt and Friedman 1979). We should also note that even inanimate objects (cans of water) "basking" in sunlight may have a negatively skewed temperature distribution (Heath 1964), and so neither a thermoregulatory capacity nor an adaptive advantage (both lacking for cans of water) need be invoked to explain observed temperatures or a negatively skewed temperature distribution.

Heliothermic lizards often have a narrow range of $T_{b,pref}$, but their **thermal performance breadth** is a wider range of T_b's for which physiological
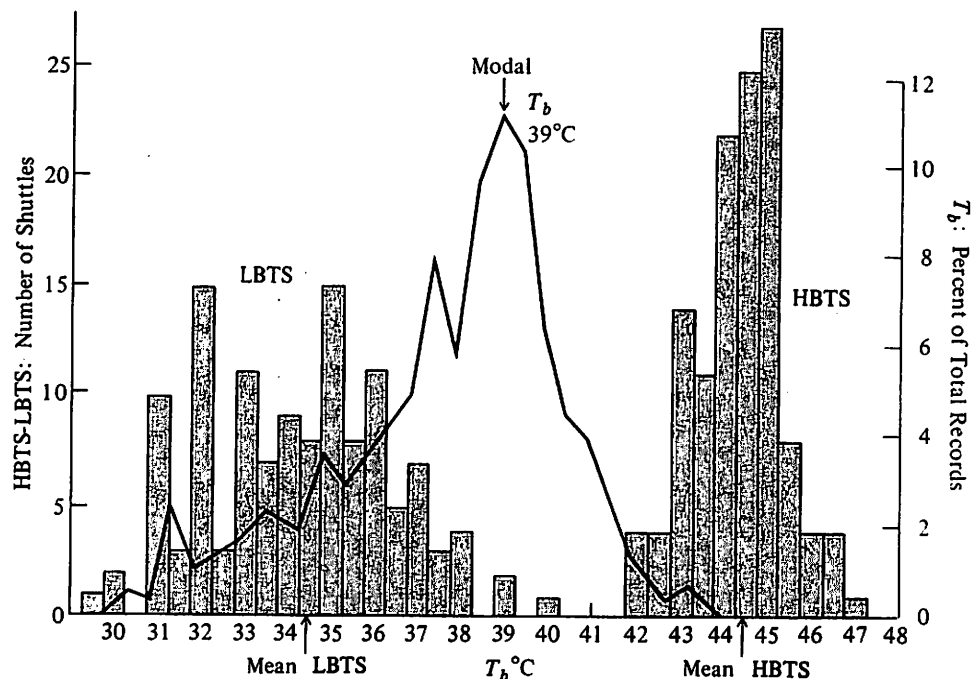
FIGURE 5–15 Frequency distribution for body temperatures of the desert iguana (Dipsosaurus) in a laboratory thermal gradient, and the frequency distributions for an individual lizard of its low body temperatures that initiate a heating cycle (LBTS) and the high body temperatures that initiate a cooling cycle (HBTS). (Modified from DeWitt 1967; Berk and Heath 1975.)

performance is "fairly high." This breadth is arbitrarily defined depending on the physiology and ecology of the species in question; the temperature range for 80% of the maximum value is a common value. The **thermal tolerance range** is the broadest range of temperatures over which the animal can survive indefinitely. Finally, the **thermal survival zone** is defined by the lethal critical thermal minimum temperature (CT_{min}) and the critical thermal maximum (CT_{max}).

There are physiological advantages to elevated T_b that explain why heliothermy and high $T_{b,pref}$ have evolved in many different animal groups. Essentially all biochemical reactions have a Q_{10} of 2 to 3 and consequently so do many physiological processes. Muscles contract faster at a higher temperature, enzymes cleave substrates faster, digestion is faster, animals can run faster and for longer periods of time, and metabolic rate is higher. There is, however, an **optimal temperature** for many of these biochemical and physiological functions, and rates plateau or decline at even higher temperatures (Figure 5–16) because of the thermal instability of protein structure and function. There generally is a close correspondence between the optimum temperature for many biochemical and physiological processes and the $T_{b,pref}$. For example, there is a marked thermal dependency of digestive efficiency for the herbivorous lizard *Dipsosaurus*: 54% at 33° C, 63%

at 37° C, and 71% at 41° C. Lizards kept at 22° C do not pass food from their stomach and die. Insectivorous lizards have a higher digestive efficiency (see also Chapter 18) and a lesser thermal dependence: 83 to 91% for 26 to 33° C (no food passed at 21° C). There is little effect of temperature on digestive efficiency for the eurythermal thigmothermic lizard *Gerrhonotus* (92 to 94% for 18° to 30° C).

Adaptations to Cold

Many ectotherms are biochemically and physiologically adapted to survive and even function normally at low ambient temperatures. However, temperatures that are cold enough to freeze animal tissues are potentially lethal and must either be avoided or require specific adaptations for survival. Many ectotherms simply avoid freezing conditions by migrating or retreating to warmer microclimates, but some occasionally or routinely experience freezing temperatures. Aquatic ectotherms can experience only mild freezing conditions, since water or seawater freezes at 0° to −2° C, and the high latent heat of fusion buffers further temperature change. Terrestrial ectotherms, in contrast, are particularly susceptible to freezing because the air temperature can fall considerably below 0° C (e.g., −20° to −50° C).
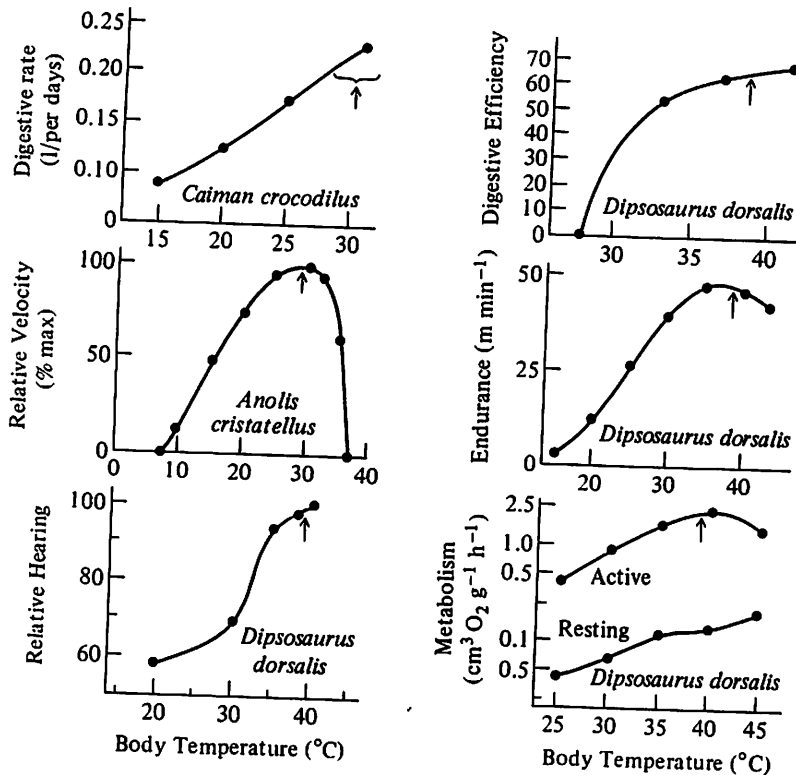

FIGURE 5–16 Relationship between various physiological functions and body temperature for reptiles, showing the general relationship between maximum physiological performance and preferred body temperature (vertical arrow). *(From various sources, as adapted by Huey 1982.)*

There are a variety of strategies that enable ecothermic animals to survive freezing conditions.

Anti-Freeze Strategy. Various ectotherms, such as polar arthropods and icefish (Figure 5-17A), avoid freezing by lowering the freezing point of their body fluids below that of the ambient medium, i.e., **freezing point depression**, or by allowing the body fluids to **supercool** below their normal freezing point. Alternatively, some ectotherms such as insects, frogs, and baby turtles allow selective extracellular freezing of their body fluids, but avoid freezing of their intracellular fluids. Let us now examine each of these strategies in more detail.

Osmotic Depression of Freezing Point. Fresh water freezes at 0° C. The freezing point of a solution is depressed below the normal freezing point of water by the presence of solute molecules. The magnitude of the freezing point depression (Δ_{fp}) is proportional to the osmolal concentration ($C_{osmolal}$) as

$$\Delta_{fp} = -1.86 C_{osmolal} \qquad (5.13)$$

Ectotherms can counteract a potentially freezing ambient temperature by increasing the osmotic concentration of their body fluids so that its freezing point is depressed below the ambient temperature. The normal body fluid concentration of ectotherms confers a very limited protection against freezing in fresh water because the freezing point of tissues is

generally $-0.6°$ to $-0.7°$ C. Animals in seawater are more prone to freezing because their tissues are generally not hyperosmotic, and therefore will freeze at the same, or a higher, temperature than seawater ($-1.86°$ C).

Some ectotherms accumulate high concentrations of specific solutes to depress their freezing point by <1 to $>10°$ C. These solutes are typically sugars (glucose, fructose, trehalose) or sugar alcohols (polyols: glycerol, sorbitol, mannitol, erythritol, myo-inositol). Their low molecular weight maximizes the freezing point depression per mass of solute. These sugars and polyols may also have cryoprotectant effects; they protect membranes and enzymes against cold denaturation and cold shock injury, inhibit lipid phase transitions, and promote desiccation resistance. Many solutes also promote supercooling. Some animals also have antifreeze proteins that induce a hysteresis between the freezing point and the melting point of the body fluids.

Supercooling. If water is cooled, its temperature is expected to decline in proportion to the rate of heat removal and the specific heat of water (4.2 J g^{-1} °C^{-1}) until ice begins to form at the freezing point ($0°$ C). The rate of temperature decline is reduced during freezing because latent heat is released by the freezing water (the latent heat of fusion is about 334 J g^{-1}). When all of the water is frozen, the temperature declines in proportion to the rate of

A   B

FIGURE 5-17 Examples of animals that use different physiological strategies for adapting to freezing ambient temperatures. (A) The supercooled icefish *Trematomus* has antifreeze proteins that reduce the freezing point of its tissues to below the freezing point of seawater. (B) The frozen wood frog *Rana sylvatica*; this frog survived when thawed. *(Photographs courtesy of: (A) Dr. Arthur L. DeVries, University of Illinois at Urbana-Champaign, 1988. (B) Courtesy of Dr. F. H. Pough, Laboratory of Functional Ecology, Cornell University, © F. H. Pough.)*

heat loss and the specific heat of ice (about 2.1 J g^{-1} $^{\circ}C^{-1}$). We might expect a similar pattern in temperature change for a cooling animal, except that the temperature would decline in proportion to the specific heat of animal tissues (about 3.4 J g^{-1} $^{\circ}C^{-1}$) and the freezing point would be lower than 0° C, depending on the osmotic concentration of the body fluids.

Pure water and solutions do not necessarily freeze at their nominal "freezing points," but may **supercool**, i.e., remain liquid at below their normal freezing temperature. For example, pure water can be easily supercooled by a few degrees, and with care to < -20° C. Similarly, animal tissues can supercool to below their expected freezing point (Figure 5–18A). The capacity to supercool seems to be a fairly general property of solutions and animal tissues. For example, many reptiles and the blood of fish, frogs, reptiles, birds, and mammals will supercool to -5° to < -10° C, although their melting temperatures are -0.4° to -1.0° C (Lowe et al. 1971). The melting temperature of ice or frozen tissues is always at its theoretical freezing temperature, determined by their osmotic concentration.

For example, the hemolymph of the supercooling insect *Bracon* has a supercooling temperature that is much lower than its theoretical freezing temperature and the melting temperature because of the accumulation of high concentrations of glycerol (Figure 5–18B).

Some ectotherms, and even an endotherm (the arctic ground squirrel), rely on their supercooling capacity to avoid freezing. For example, benthic fish in the fjords of Labrador supercool below their body fluid freezing point (about -0.7° C) to a T_b near -1.86° C, the freezing point of seawater (Scholander et al. 1953). Contact with exogenous ice crystals, for example at the gills, would "seed" the supercooled body fluids and initiate rapid freezing of the entire fish, but this does not normally occur because the fish are benthic and do not come into contact with ice crystals in the water, since ice floats.
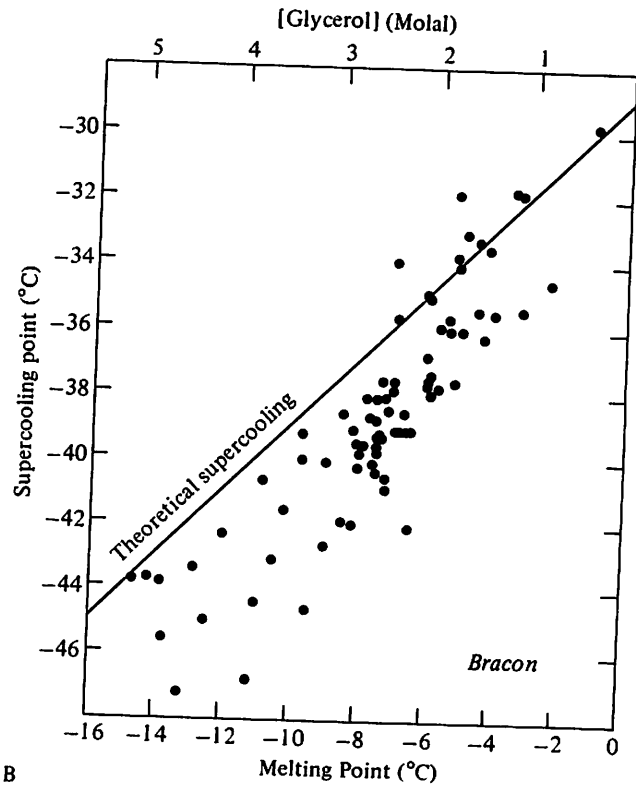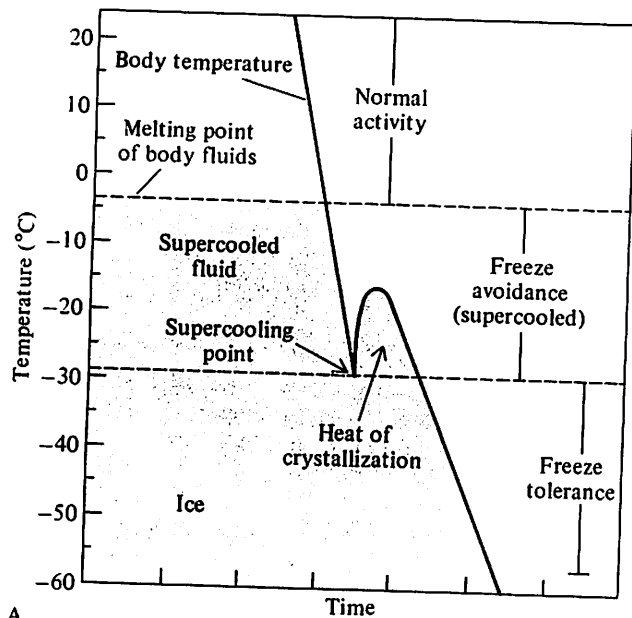
FIGURE 5–18 (A)   Schematic response of an animal to cooling to subfreezing temperatures. The body temperature declines to below the freezing point, i.e., supercools. When freezing is initiated, the heat of crystallization is released and temporarily increases the temperature. After all fluid is frozen, the tissue continues to freeze. (B) Relationship between the supercooling point and melting temperatures for the hemolymph of a cold-hardy parasitic wasp, showing also the theoretical concentration of glycerol required to depress the supercooling point by a constant amount.   (From Lee 1989; modified from Salt 1959.)

Overwintering insects are generally categorized as either freezing intolerant or freezing tolerant. Many freezing-tolerant species have a spectacular capacity to supercool to avoid tissue freezing, and some are also tolerant of tissue freezing (Baust 1986). They produce an often complex array of low molecular weight antifreeze osmolytes that depress the freezing point and lower the supercooling temperature and cryoprotective solutes (Table 5-7).

The few studies of cold resistance in spiders indicate that they can supercool to -20° C and

below (Kirchner 1973). The capacity to supercool is proportional to the location of the overwintering sites and the likely extent of cold stress. The lowest supercooling temperatures are for spiders overwintering in vegetation (-16° to -26° C) or under tree bark (-13° to -15° C). The highest supercooling temperatures are for spiders overwintering in caves or under stones (-4° to -8° C). Whether, or what, antifreeze proteins, polyols, or other osmolytes are involved in supercooling is unclear. Glycerol and hemolymph proteins are not

TABLE 5-7

Supercooling temperatures and accumulated solutes for a variety of ectothermic invertebrates and vertebrates that are exposed to freezing conditions. The approximate concentrations of solutes in the hemolymph or plasma (h), whole body water (wbw), or whole body (wb) are also indicated. AFP, antifreeze protein; INP, ice nucleating protein; INLP, ice nucleating lipoprotein; glyc, glycerol; sorb, sorbitol; tre, trehalose; ery, erythritol; glu, glucose; ala, alanine; aa, amino acids.

Species	SCT (°C)	Solutes
Spiders		
Sac spider *Clubiona*	-15.4	glyc (4.4%^{h}), AFP
Crab spider *Philodromus*	-26.2	glyc (3.3%^{h}), AFP
Insects		
Fly *Xylophagus*	-6.0	sugars (5.9%^{wbb}), aa (0.8%)
Beetle *Pytho*	-6.6	glyc (4.5%^{wb}), sugars (1.4%)
Crane fly *Tipula*	-7	sorb (0.4 M), INP, INLP
Gall fly *Euura*	-7.1	no glyc
Sawfly *Trichiocampus*	-8.6	tre (9%^{h})
Carabid beetle *Pterostichus*	-10.0	glyc (25%^{h})
Darkling beetle *Meracantha*	-10.3	AFP
Goldenrod gall fly *Eurosta*	-10.3	glyc (5.9%), sorb (9.1%), tre (0.4%)
Pyrochroid beetle *Dendroides*	-12	glyc (14%^{h}), sorb (2.5%), AFP
Wooly bear *Isia*	-18.2	glyc (4.44%^{wb}), sorb (0.83%)
Grain moth *Nemapogon*	-26.1	tre (0.2m^h), ala (0.07M)
White cabbage butterfly *Pieris*	-26.2	tre (0.08M^h), ala 0.07M)
Leaf-cutter bee *Megachile*	-27.7	glyc (2,2% ^{wbw})
Carpenter ant *Camponotus*	-28.7	glyc (5.8%^{wbw})
Mite *Alaskozetes*	-30	polyols (3-5%^{wb}), glyc (0.5M)
Tortricid moth *Laspeyresia*	-31.5	glyc (0.5M^h), tre 0.1M)
Bark beetle *Ips*	-32.4	ethylene glycol (2.9M)
Rose root gall fly *Diplolepis*	-32.7	glyc (6.4%^{wbw})
Pine beetle *Dendorctonus*	-34	glyc (23.4%^{wbw})
Wasp *Bracon*	-41.2	glyc (2.7M^{wbw})
Willow aphid *Pterocomma*	-41.9	glyc (15.5%^{wbw})
Cankerworm *Alsophila*	-44.6	glyc (15.5%^{wbm})
Gall midge *Rhabdophaga*	-49.1	glyc (32.4%^{wbw})
Wasp *Eurytoma*	-49.2	glyc (23.4%^{wbw})
Beetle *Pytho*	-54	glyc (13.2%^{wb}), sugars (5.5%)
Vertebrates		
Gray tree frog *Hyla*	-2.0	glu (0.02M^h)
Chorus frog *Pseudacris*	-2.0	glu (0.06M^h)
Spring peeper *Hyla*	-2.2	glu (0.18M^h)
Wood frog *Rana*	-3.0	glu (0.41M^h)
Turtle	-3.3	glu (0.01M^h), aa (0.047M)
Arctic ground squirrel	-2.9	none (?)

involved with supercooling in *Araneus*. The hemolymph of the crab spider (*Philodromus*) and sac spider (*Clubiona*) in winter contain a thermal hysteresis protein (i.e., antifreeze protein, AFP) and glycerol (see below).

Little is known of the mechanisms for cold resistance in terrestrial gastropods, e.g., pulmonate snails. The snail *Arianta* survives subzero temperatures by supercooling to −3.5° to −9° C (Stover 1973). These snails have some tolerance to tissue freezing, which is greater in winter than summer and in high altitude populations, but the tolerance is minimal and is probably of little adaptive significance in nature.

Antifreeze Proteins. Antarctic fish can't rely on supercooling because ice frequently occurs in their environment, both at the surface and at the ocean bottom. The freezing point of their body tissues can be as low as −2.7° C (which provides complete protection against freezing in seawater) but the melting temperature is only about −0.9° C (Table 5–8). The lowered freezing point and the hysteresis between freezing point and melting point are attributed to specific "antifreeze" proteins in the blood and other body fluids. The extent that fish antifreeze proteins depress the melting temperature depends on their molal concentration as expected, whereas the freezing point is lowered in a noncolligative

manner (i.e., the freezing point depression is not proportional to the osmotic concentration). The antifreeze proteins of most antarctic fish and some northern fish are glycoproteins (AFGP), and for other polar fish are proteins (AFP). Similar AFPs are responsible for a thermal hysteresis in freezing and thawing temperature for some spiders and insects.

Antifreeze glycoproteins are polymers of a repeating tripeptide (alanyl-alanyl-threonine) linked to a galactose-N-acetylgalactosamine carbohydrate moiety; repetition of up to 50 of these subunits results in a molecular weight from 2.6 to 33 10^3 Da (Figure 5–19A). There is minor variation among small AFGPs with proline and/or arginine replacing alanine or threonine at some positions. The AFGPs of the Antarctic nototheniid *Pagothenia borchgrevinki* vary in molecular weight; 32700 (AFGP1), 28800 (AFGP2), 21500 (3), 17000 (4), 10500 (5), 7900 (6), 3500 (7), and 2600 (8).
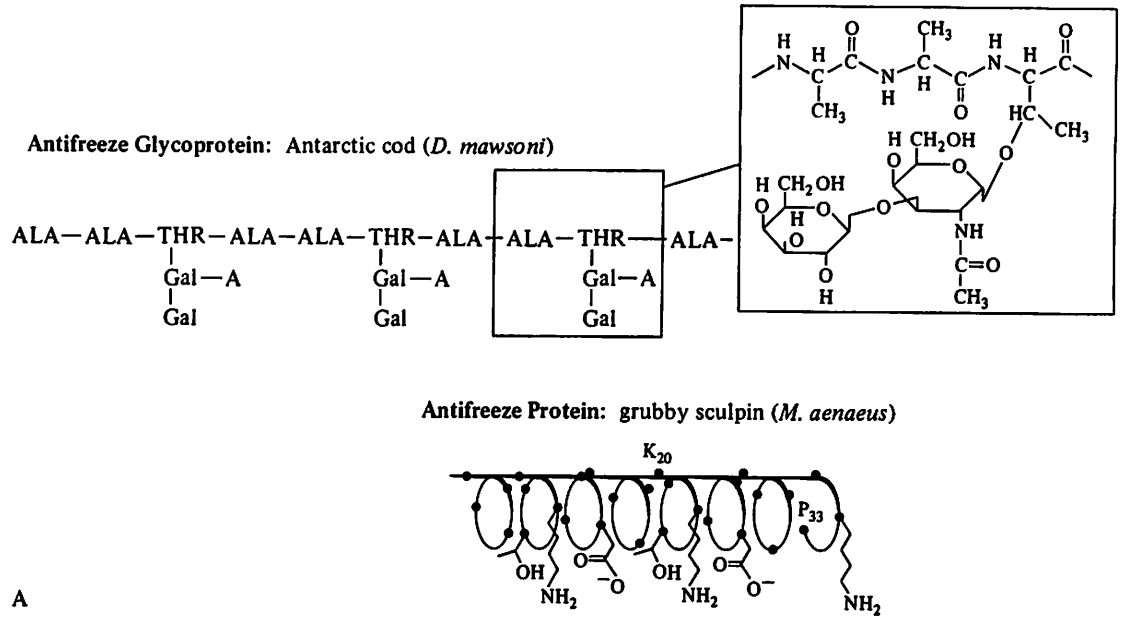
Antifreeze proteins (AFPs) lack a carbohydrate moiety. They vary considerably in structure, but there are three general types: those containing much alanine (e.g., winter flounder, shorthorn sculpin) with an α-helical structure and molecular weight from 3.3 to 4.5 10^3 Da (Figure 5–19A); those containing much cystine (e.g., sea raven) and a β-structure with molecular weight 11 to 13 10^3 Da; and the remainder that are neither alanine or cystine rich, with a compact structure and molecular weight of 6 10^3. The three AFPs (1,2,3) of the Antarctic eel pout *Rhigophila* have a molecular weight of 6900 but differ in amino acid residues.

Antifreeze proteins depress the freezing temperature (but not the thawing temperature) by about −0.6° C. This freezing point depression is 200 to 300 × that expected from their osmotic concentration (Figure 5–19B). The maximum freezing point depression is about −120° C/osmolal (cf. about −1.86° C/osm for NaCl). On a mass basis, all of the glycoproteins have a similar capacity for freezing point depression except the highest molecular weight AFGPs, which are less effective. However, all antifreeze proteins (AFGPs and AFPs) are slightly more effective on a mass basis than NaCl in depressing the freezing point to a concentration of about 10 g l^{-1}; but are less effective at higher concentrations.
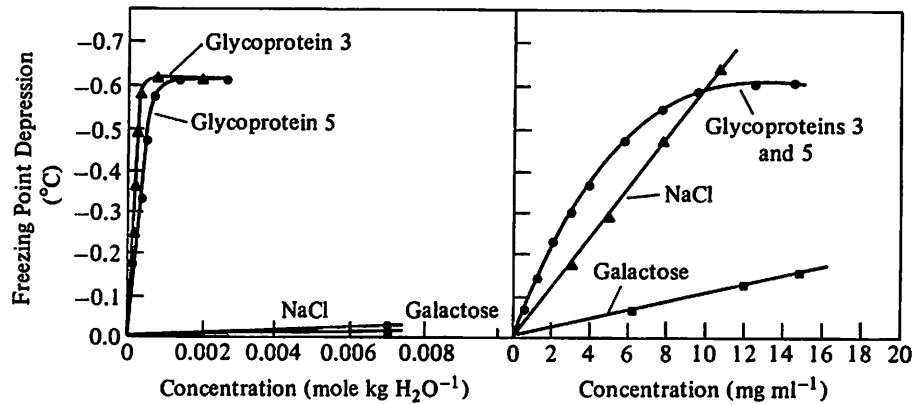
A high concentration of polar groups facilitates a strong interaction of antifreeze proteins with ice crystals and inhibits the further addition of water molecules to the ice front, thereby "poisoning" the growth of an ice crystal. This binding to ice crystals is suggested by the fact that antifreeze proteins do not freeze out of solution (i.e., do not become

TABLE 5–8

Thermal hysteresis in freezing temperature and melting temperature for hemolymph of spiders and insects and for plasma of icefish.			
	Freezing Temperature	Melting Temperature	Thermal Hysteresis	Supercooling Temperature
Fish				
Gadus	−1.1	−0.7	0.4	
Chaenocephalus	−1.5	−0.9	0.6	
Rhigophalia	−2.0	−0.9	1.1	
Myxocephalus	−2.0	−1.1	0.9	
Notothenia	−2.1	−1.1	1.0	
Eleginus	−2.2	−1.2	1.0	
Pagothenia	−2.7	−1.1	1.6	
Spiders				
Philodromus	−5.19	−2.74	2.45	−26.2
Clubiona	−4.76	−2.87	1.89	−15.4
Insects				
Meracantha	−5.01	−1.31	3.71	−10.3
Dendroides	−7.03	−3.37	3.66	−9.5

Antifreeze Glycoprotein: Antarctic cod (*D. mawsoni*)

ALA—ALA—THR—ALA—ALA—THR—ALA—ALA—THR——ALA—
        | | |
        Gal—A   Gal—A   Gal—A
        | | |
        Gal   Gal   Gal

Antifreeze Protein: grubby sculpin (*M. aenaeus*)

K_{20}

P_{33}

A

B

FIGURE 5–19 (A)   Schematic structure of the antifreeze glycoprotein (AFGP) of the antarctic cod (*Dissostichus mawsoni*) and a schematic representation of part of the antifreeze protein of the grubby sculpin (*Myoxocephalus aenaeus*) showing the hydrophilic side chains extending below the hydrophobic α-helix chain. (B) Freezing point depression as a function of osmolal concentration (mole kg water^{-1}) and mass concentration (mg ml^{-1}) for antifreeze glycoproteins, sodium chloride, and galactose.   *(From DeVries 1980b; Chakrabartty and Hew 1988; DeVries 1971.)*

concentrated in the remaining liquid water as do normal colligative solutes) but are frozen into the ice.

Antifreeze proteins may prevent the entry of ice crystals across the gills, integument, or gut of ice fish, but there is evidence that ice crystals are normally present in their body tissues. Fish taken from the ice water environment and cooled to −2.7° C will rapidly freeze. This is not because attached

ice crystals of seawater precipitate tissue freezing, because the fish will still freeze even if they are initially kept at − 1.2° C (which would melt seawater ice crystals but not body fluid ice crystals). If the fish are initially kept at 0° C (to melt all ice crystals, whether seawater or body tissues), then the fish can supercool to −7° C. The body ice crystals are apparently not in the blood (which will not freeze at −2.7° C) but elsewhere.

Antifreeze proteins are synthesized in the liver and are secreted into the circulation for distribution to most of the other body fluid compartments except the intracellular fluid, the endolymph (inner ear fluid), and the urine. Antifreeze proteins are present at low concentrations in pericardial, peritoneal, extradural, and cerebrospinal fluid and at very low concentrations in the ocular fluid. Presumably antifreeze proteins are not required in fluid compartments that are surrounded by antifreeze-protected fluids, e.g., intracellular and intraocular fluid (it is not clear why CSF has antifreeze proteins, since it is similarly protected by surrounding extracellular fluids).

Urine is not antifreeze protected, and is therefore normally supercooled by about 1° C. The urine lacks antifreeze proteins because (1) the kidneys are aglomerular and antifreeze proteins are not secreted into the tubule, e.g., Nototheniids; or (2) the filtration barrier is thick and Bowman's capsule is not connected to the nephron tubule, e.g., the Antarctic eel pout; or (3) charge repulsion prevents filtration of the acidic AFP across the anionic filtration barrier, e.g., northern winter flounder.

Freezing Tolerance. A number of invertebrates, and a very few vertebrates, are able to tolerate the freezing of a significant fraction of their body water (Figure 5–20). The few freeze-tolerant frogs and reptiles can tolerate less ice formation (35 to 50% frozen) than intertidal mollusks (54 to 76%) and insects (>90%).

It is important in these frozen animals that the freezing of body water is restricted to the extracellular fluids. For example, the cells of frozen intertidal mollusks are shrunken and distorted, but do not contain ice crystals (Kanwisher 1955). Ice crystal formation in the intracellular fluids inevitably results in death. Intracellular ice crystals apparently destroy the integrity of intracellular membranes and organelles. In contrast, extracellular freezing does not disrupt essential cell structures and is not lethal (at least to the freeze-tolerant species).

The ability of tissues to avoid intracellular freezing depends on the rate of cooling; rapid cooling promotes intracellular freezing (Mazur 1963). It is potentially disadvantageous, therefore, for freeze-tolerant animals to supercool, because when freezing occurs it is rapid and likely to occur in the intracellular fluids as well as the extracellular fluids. Consequently, a number of freeze-tolerant animals contain specific **nucleating agents** that promote freezing and retard supercooling. Freeze-tolerant frogs (see Figure 5–17B) do not have nucleating agents, but their large size (1 to 15 g) ensures that they cool
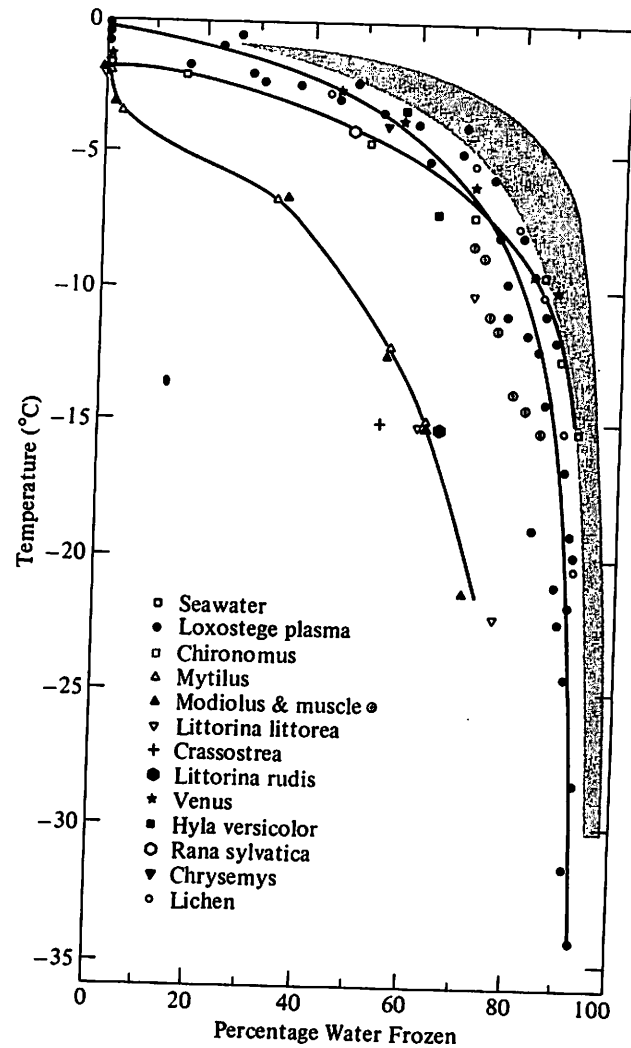

FIGURE 5–20 Percentage of water frozen as a function of temperature for seawater, plasma of an insect (*Loxostege*), insect larvae (*Chironomus*), marine mollusks (*Mytilus, Crassostrea, Modiolus, Littorina, Venus*), frogs (*Hyla, Rana*), and a lichen (*Cetraria*).

slowly, minimizing the likelihood of supercooling (Storey 1986). The extracellular water of their limbs freezes first (the limbs would cool faster because of their higher surface:volume ratio). Ice crystals then form under the skin and become interspersed with leg muscles, and a large mass of ice fills the abdominal cavity. The frozen frog has no respiratory cycle, no (or only infrequent) heart beat, and frozen blood.

Freezing of the extracellular fluid has severe osmotic consequences for the intracellular environment. As the extracellular fluid freezes, ions and other solutes tend to remain in solution in the unfrozen fluid, hence the osmotic concentration of the unfrozen water increases. Intracellular water

would be osmotically withdrawn from the intracellular space by the elevated extracellular osmotic concentration. There is generally an exponential relationship between the percentage ice content and temperature (Figure 5–20), and this results in a fairly linear relationship between the osmotic concentration of the extracellular fluid and temperature (Scholander et al. 1953). Thus, freeze-tolerant animals must also be very dehydration tolerant. For example, a marine mollusk with 75% of its water frozen would have an osmotic concentration in the remaining 25% of the unfrozen water of 4 × seawater. Seasonal acclimation of freezing tolerance in intertidal mollusks involves greater tolerance of tissue dehydration and elevation of body fluid osmotic concentration, rather than reduction of the amount of water lost from the cells. For example, *Modiolus* acclimated to 23° C die when 35% of their intracellular water is osmotically withdrawn into the partially frozen extracellular space, but animals acclimated to 0° C can tolerate an even higher loss of 41% intracellular water (Murphy and Pierce 1975). In contrast, adaptation to low salinity (12‰) decreases the percentage of frozen water and the freezing tolerance of *Modiolus* (to −5.1° C) compared to −10.3° and −12.2° C at 34 and 46‰. The high freeze tolerance of these animals may involve polyols (like glycerol) acting as cryoprotectants.

Adaptations to Heat

Ectotherms exposed to high temperature can either attempt to regulate their T_b below the T_a or rely on biochemical adaptations for tolerance of high T_b. The former strategy of thermoregulation can only be accomplished by evaporative cooling, hence is unavailable to aquatic animals. The second strategy increases the upper lethal temperature (CT_{max}).

Critical Thermal Maximum. The ultimate thermal limit for living cells is the boiling point of water (100° C at normal atmospheric pressure). No animals or plants are able to survive temperatures approaching the boiling point, but some prokaryotic organisms tolerate temperatures close to the boiling point. For example, thermophilic bacteria live in the Yellowstone Hot Springs, close to the boiling point of 93.3° C (the high altitude lowers the boiling point). Eukaryotic organisms are much more sensitive to high temperature. A few animals have maximum temperatures of 50° C or greater, but most animals have a lower CT_{max} (Table 5–9).

The upper thermal limit can be measured in a variety of ways, but the lethal temperature for 50%

TABLE 5–9

Critical thermal maximum (CT_{max}) for a variety of invertebrates and vertebrates.			
Invertebrates		**Vertebrates**	
Prokaryotes		**Fish**	
Bacteria		*Fundulus*	35
Aquatic	73		
Thermophilic	91	**Amphibians**	
Bluegreen algae	75	Salamanders	
		Rhyacotriton	29
Echinoderms		*Plethodon*	31.5
Asterias	32	*Ensatina*	34
Ophioderma	37	*Aneides*	34.3
Arbacia	37	*Ambystoma*	35.6
		Anurans	
Annelids		*Hyla*	36
Lumbricus	29	*Rana*	37
		Eupemphix	37.8
Crustaceans		*Bufo*	41
Palaemonetes	34		
Porcellio	39.0	**Reptiles**	
Uca	39.5	Alligator	38
Porcellio	41.0	Turtles	41
Armadillidum	41.4	Lizards	43.4
Uca	45.2	Xantusids	40.1
		Scincids	41.2
Mollusks		Varanids	42.0
Modiolus	37.8	Anguids	42.4
Nassa	42	Helodermatids	42.5
Clavarizona	43	Gekkonids	43.7
		Iguanids	45.0
Insects		Agamids	45.4
Lepisma	36	Teids	46.0
Thermobia	>40	Pygopodids	46.0
Sphingonotus	41	Acertids	46.9
Bembex	42	Snakes	40.4
Aiolopus	45	Elapids	40.4
Trigonopus	45	Crotalids	41.3
Ctenolepisma	48	Colubrids	41.6
Onymacris	49		
Onymacris	50		
Onymacris	51		
Dasymutilla	52		
Arachnids			
Buthotus	45		
Leiurus	47		

mortality (LT_{50}; see Chapter 2) is one common measure. Both the temperature and the time of thermal exposure are important determinants of LT_{50}. For example, heat death occurs in the starfish *Asterias* after 40 min at 32° C, but after only 9 min at 42° C; the times to heat death for the gastropod *Nassa* are 30 min at 42° C but only 9 min at 46° C. An index of thermal incapacitation, rather than death, is often used to define an upper critical

temperature. For example, the temperature at which an animal loses its coordination and locomotor ability is often defined as the CT_{max}. The maximum temperature that an animal will voluntarily select is called the experimental voluntary maximum (T_{EVM}). A panting threshold temperature (T_{PT}) may be used to indicate heat stress. The temperature for onset of muscle spasms (T_{OMS}) is another possible index to define a CT_{max}, as is the temperature for cessation of breathing (T_{CB}).

Most invertebrates and vertebrates have CT_{max} values over 30° C, and some have CT_{max} values over 40° C (Table 5–9). CT_{max} is generally consistent within a taxonomic group, e.g., scincid lizards have a lower CT_{max} than lacertid lizards, but there is considerable variability within a taxonomic group according to habits and thermal environment. For example, temperate fossorial skinks have lower CT_{max} than terrestrial skinks and fossorial desert skinks. The CT_{max} is lower for forest anole lizards than open habitat species; edge species have intermediate CT_{max} (Table 5–10). Ambient relative humidity also affects the CT_{max}, which is generally lower in humid air than in dry air. CT_{max} also varies latitudinally for anuran amphibians. CT_{max} is different for larval and adult amphibians; *Rana pipiens* tadpoles are more sensitive to high temperature than are the adults. Furthermore, different tissues may have varying thermal sensitivity. The skeletal muscle of *R. pipiens* has about the same thermal tolerance as the intact adult, but sciatic nerve and heart have a higher thermal tolerance. Acclimation temperature also influences the CT_{max} (see below).

TABLE 5–10

Effects of habitat on critical thermal maximum (CT_{max}) in closely-related anole lizards *(Anolis)*. *(Data from Hertz 1979.)*	
Open Habitat	
A. cooki	38.9
A. cybotes	39.3
A. cristatellus	39.4
A. auratus	40.0
A. carolinenis	40.7
Edge Habitat	
A. tropidogaster	33.4
A. frenatus	35.7
A. krugi	36.0
Forest Habitat	
A. limifrons	33.4
A. gundlachi	34.5

Evaporative Cooling. Evaporation of water dissipates heat (2456 J g^{-1} at 20° C, 2432 at 30° C, 2408 at 40° C, and 2260 at 100° C). Consequently, evaporative water loss can dissipate a considerable amount of heat and lower the temperature. The extent of evaporative cooling depends on the ambient relative humidity and temperature. For example, objects that evaporate water as if they were a free water surface have a wet bulb temperature that is lower than the dry bulb air temperature. The wet bulb temperature is that measured by a thermometer with a moist covering, with maximum forced convection. The dry bulb temperature is the normal air temperature, with no evaporative cooling effect.

The skin of many ectothermic invertebrates and vertebrates evaporates water as if it were a free water surface, and these animals act as wet bulb thermometers. For example, most frogs, toads, and slugs have T_b closer to T_{wet} than to T_{dry} (Figure 5–21). Active snails (or snails with their shell removed) have T_b similar to T_{wet}, but inactive snails withdrawn into their shell have T_b closer to T_{dry}. Earthworms have T_b similar to T_{wet}, but T_b is closer to T_{dry} if their skin becomes desiccated. Fiddler and ghost crabs can have a T_b 3° to 4° C lower than T_{dry}. The T_b of the isopod *Ligia* can be depressed by as much as 8° C, but more terrestrial species have lower rates of water loss and a lesser T_b depression (4° C for *Porcellio* and 4° to 5° C for *Oniscus*). Some bivalves, such as *Modiolus*, maintain a 1° to 2° C temperature gradient by keeping their valves partly open. These animals are passive evaporators; their T_b depression is not an active thermoregulatory response. However, some ectotherms have mechanisms to keep their skin moist during evaporation. For example, some frogs frequently discharge skin mucous glands to prevent dehydration of the skin, and a high cutaneous blood flow maintains the hydration level of the skin. Terrestrial ectotherms tend to have reduced cutaneous evaporation to prevent rapid dehydration, e.g., terrestrial isopods, crustaceans, waterproof frogs, and lizards (see Chapter 16). Their T_b is normally closer to T_{dry} than to T_{wet} (e.g., reptiles; Figure 5–21).

Relatively waterproof terrestrial animals are generally able to enhance evaporative cooling for T_b regulation at high T_a by markedly increasing their cutaneous or respiratory water loss. For example, the lizard *Dipsosaurus* totally dissipates its metabolic heat production by panting at T_a >40° C, although it is not able to significantly reduce its T_b below T_a. In contrast, the large agamid lizard *Amphibolurus* can reduce its T_b about 3.2° C below T_a (42.5° C). The chuckwalla *Sauromalus* can reduce
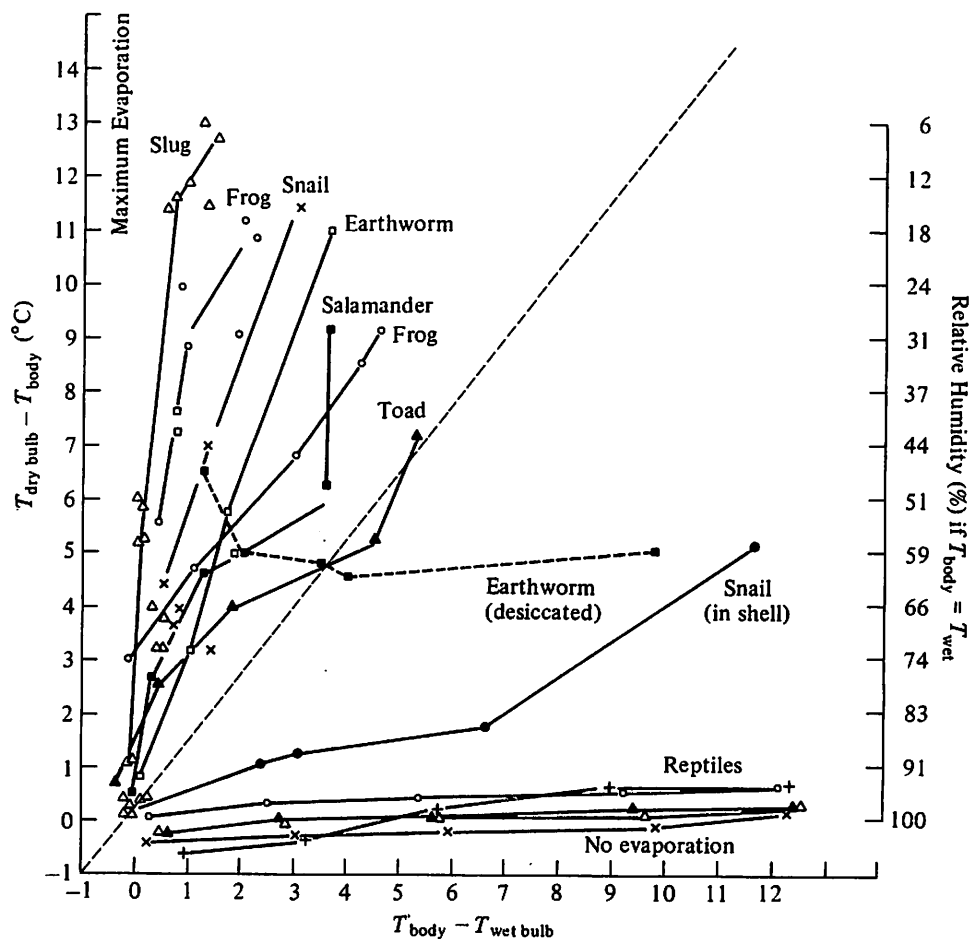
FIGURE 5–21 Body temperatures of some invertebrates and vertebrates graphed as a function of the difference between body temperature (T_b) and wet bulb temperature (T_{wet}), and the difference between body temperature and dry bulb temperature (T_{dry}). The ordinate ($T_b - T_{wet} = 0$) indicates the maximum extent of evaporative cooling and the abscissa ($T_b - T_{dry} = 0$) indicates no evaporative cooling.

its T_b about 0.9° C below T_a (at 45° C) and brain temperature (T_{br}) about 2.7° C below T_a by evaporative cooling by panting (Figure 5–22). A chuckwalla prevented from panting, or a dead lizard, has T_b and T_{br} similar to T_a.

The waterproof frogs *Chiromantis* and *Phyllomedusa* have markedly lower evaporative water loss than other frogs, consequently their T_b is similar to T_a, but is lower at high T_a (Figure 5–23). Both *Chiromantis* and *Phyllomedusa* can dramatically increase water loss when heat stressed to precisely regulate T_b below T_a. *Chiromantis* discharges cutaneous mucous glands to elevate evaporation water loss. *Phyllomedusa*, in contrast, is waterproofed by an epidermal wax layer; its EWL increases when the epidermal wax layer melts at high T_a (McClanahan,

Stinner, and Shoemaker 1978); there is also a mucous gland discharge that contributes to the increased evaporative water loss (Shoemaker et al. 1987).

Advantages of Ectothermy

There are a number of thermal and energetic advantages to ectothermy (Pough 1980). We need to distinguish two types of ectotherms: (1) eurytherms that do not thermoregulate (at least very well) and whose T_b is similar to T_a and (2) stenotherms that thermoregulate T_b precisely within a narrow range using heliothermy or thigmothermy.

The primary advantage of eurythermal ectothermy is that no metabolic energy or time is
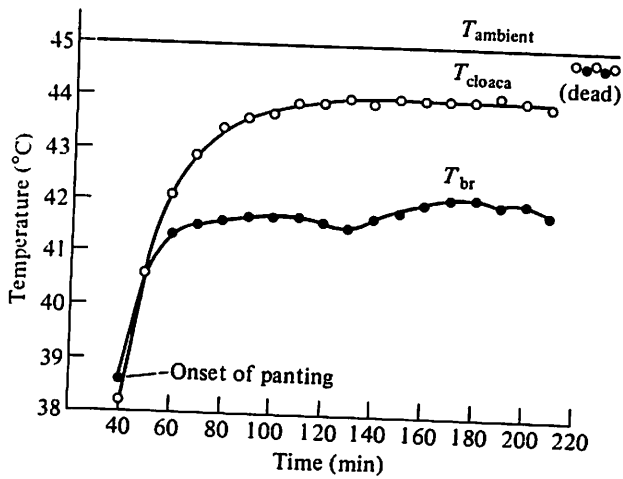
FIGURE 5–22 The body temperature (T_b) and brain temperature (T_{br}) of the chuckwalla lizard *Sauromalus obseus* are considerably lower than the ambient temperature ($T_{ambient}$) of 45° C; the T_b and T_{br} of a dead lizard are about 0.5° C below $T_{ambient}$ because there is some evaporative heat dissipation. *(From Crawford 1972.)*

experienced by a eurythermal ectotherm. Many physiological functions (locomotion, digestion, growth, excretion, membrane and action potentials) are similarly compromised over a wide range of temperatures. Thus, a "jack-of-all-temperatures" may be a master of none (Huey and Hertz 1984).

A stenothermal ectotherm precisely thermoregulates using behavioral means when environmental conditions are appropriate, and can have as high and precisely regulated T_b as endotherms. There is no direct metabolic cost to these ectotherms because most of the heat required for thermoregulation is from solar radiation, but there may be costs for shuttling movement (Huey and Slatkin 1976). Stenothermal ectotherms have a metabolic rate about 1/10 that of endotherms of the same size at the same T_b. Furthermore, the T_b of stenothermic ectotherms declines during the night and further depresses metabolic rate. Consequently, the daily energy expenditure of stenothermal ectotherms is only about 1/20 that of endotherms, and the ectotherm can convert much more of its energy intake into production (growth, reproduction) rather than metabolism (see Chapter 4). However, there are costs and disadvantages to stenothermal ectothermy. Activity is limited by daily and seasonal solar radiation cycles; digestion can be limited by low body temperatures during the inactivity phase; there is a time and energy cost for thermoregulatory activities; realized field T_b values may not be equal to either

expended on thermoregulation, but there are biochemical, physiological, and energetic disadvantages. For example, enzyme systems cannot function optimally over the wide range of body temperatures
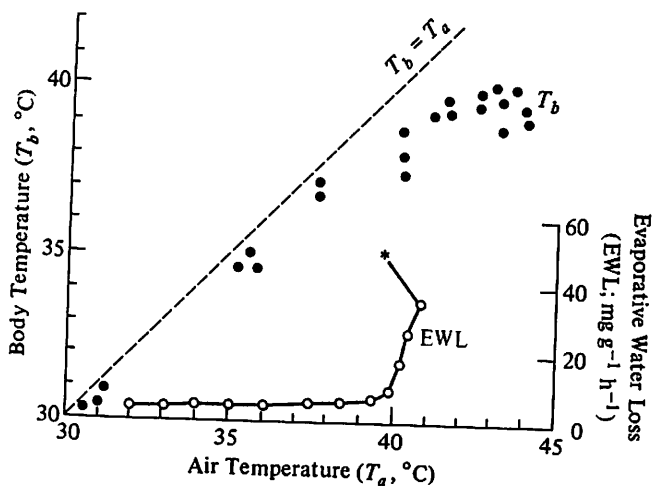

FIGURE 5–23 The body temperature (T_b; solid symbols) of the waterproof frog *Phyllomedusa sauvagei* increases linearly with air temperature to about 38° C when T_b is regulated lower than T_a. The evaporative water loss (EWL; open symbols) is low until temperature regulation begins; EWL increases markedly when the frog moves (*). The increase in EWL is a consequence of glandular secretion, appearing in the photograph as beads of water. *(From Shoemaker et al. 1987.)*

the physiologically or ecologically optimum temperatures, depending upon ambient conditions. Few ectotherms can sustain a high aerobic capacity for prolonged periods and tend to rely on anaerobic metabolism for burst activities.

Endotherms

Endotherms derive all (or most) of their heat content from metabolic heat production, rather than from the external environment. Endogenously produced metabolic heat can allow precise regulation of T_b and most endotherms are also good thermoregulators (although this isn't a necessary consequence). The extent of thermoregulation is indicated by both the intercept value and the slope for the relationship $T_b = a + bT_a$. For thermoconformers, a is close to 0° C and b is about 1, whereas a is about 20 to 40 and b is about 0 for thermoregulators (Table 5–11).

Let us now examine patterns of endothermy for various animals, then we will consider the more speculative questions of why endothermy evolved, how it evolved, and why the T_b of endothermic animals is commonly in the 35° to 40° C range.

Mammals and Birds

Mammals and birds are endothermic, with a high and precisely regulated T_b (35° to 42° C). Partly because of this, birds and mammals were originally classified (by Owen in 1866) as members of a single taxon, the Haemothermia. This classification scheme has been rejected by virtually all zoologists in this century in favor of a separate derivation of birds from theropod archosaurs (hence birds are closely related to dinosaurs and crocodilians) and mammals from synapsid reptiles (and therefore mammals are not closely related to birds). Mammals and birds must have independently evolved endothermy. The taxon Haemothermia has recently been resurrected (Gardner 1982) but is this generally rejected as an outrageous hypothesis (Kemp 1988). We shall examine endothermy of mammals and birds together, despite their separate evolution, since both groups have essentially the same pattern of thermoregulation.

Body Temperature. Birds and mammals have independently evolved a similar pattern of endothermic physiological regulation, but there is considerable variation in their T_b (Figure 5–24). Monotremes typically have the lowest T_b of mammals (28° to 32° C); edentates also have low T_b's (33° C). Marsupials

TABLE 5–11

Coefficients for the relationship between body temperature (T_b) and ambient temperature (T_a) of the form $T_b = a + bT_a$ for animals and a plant (*Philodendron*) that thermoconform or thermoregulate, and an inanimate object (water-filled metal can) that passively responds to the thermal environment.			
	a	**b**	**Comments**
Forest anole lizard	−3.8	1.17	Ectothermic
Tenebrionid beetle	1.3	1.01	Ectothermic
Aquatic salamander	0	1.0	Ectothermic
Asian honeybee	18.3	0.81	Endothermic
Male diamond python	9.6	0.67	Ectothermic
Bullfrog	12.0	0.60	Ectothermic
Nonbrooding diamond python	14.5	0.48	Ectothermic
Desert cicada	24.8	0.44	Ectothermic
Open habitat anole lizard	16.4	0.43	Ectothermic
Dragonfly	26.3	0.43	Ectothermic
Naked mole rat	20.6	0.41	Endothermic
Sphinx moth caterpillar	23.7	0.40	Ectothermic
Water-filled metal can	24.3	0.30	Passive
Cuculinid moth	30.8	0.28	Endothermic
Bluefin tuna	25.5	0.24	Endothermic
Planigale marsupial	27.4	0.21	Endothermic
Dragonfly	35.1	0.21	Endothermic
Philodendron	38	0.18	Endothermic
Poorwill	33.6	0.17	Endothermic
Brooding diamond python	28.0	0.12	Endothermic
Pocket mouse	35.4	0.081	Endothermic
Honey possum	35.1	0.07	Endothermic
Queen bumblebee (brooding)	35.0	0.07	Endothermic
Cactus mouse	35.8	0.059	Endothermic
Chilean tinamou	35.4	0.05	Endothermic
House finch	40.0	0.05	Endothermic
Parrot	39.9	0.05	Endothermic
Rosy finch	41.0	0.02	Endothermic
Amazonian parrot	40.9	0.01	Endothermic
Least weasel	39.5	0	Endothermic
Mallee fowl	40.3	−0.04	Endothermic

and insectivores (excluding shrews) have a low T_b of about 34° to 36° C. Members of a number of mammalian orders have mean T_b values about 37° C (e.g., bats) or 38° C (primates). Among birds, the more primitive ratites have low T_b's (38° to 39° C). There is a considerable diversity in the mean T_b for various groups of nonpasserine birds, T_b may be less than 40° C (penguins), 40° to 41° C (owls), 41° to 42° C (parrots), or 42° C (woodpeckers). Passerine birds have a T_b of about 42° C.

The T_b of endotherms is essentially determined by mass-specific metabolism and thermal conductance. Birds, especially passerines, have a lower thermal conductance than mammals (Aschoff 1981).

Mammals: $C = 20.5\,g^{-0.426}$

Nonpasserine birds: $C = 19.0\,g^{-0.583}$ (5.14)

Passerine birds: $C = 11.6\,g^{-0.576}$

where C is thermal conductance ($J\,g^{-1}\,hr^{-1}\,{}^{\circ}C^{-1}$) and g is body mass in grams. The scaling of VO_2 and C varies for mammals, nonpasserine birds, and passerine birds. We would expect a variation in their T_b since $VO_2/C = 3.1\,M^{0.186}$ (mammals), $4.9\,M^{0.303}$ (nonpasserines), and $13\,M^{0.298}$ (passerines). Consequently, passerines should have a higher T_b than nonpasserines which should have a higher T_b than mammals. We would also expect a slight mass-dependence of T_b, although there is not any obvious relationship between T_b and mass for mammals or birds.

There are differences in allometric scaling of VO_2 and C for activity and resting phases of the circadian cycle, and so we might expect a corresponding circadian cycle in T_b. For example, the T_b of the gray jay *Perisoreus* is about 41.2° C during the night (when VO_2 is lower) and 42.4° C during the day (when VO_2 is higher; Veghte 1964).

Body Temperature Regulation. The endothermic mechanisms of mammals and birds are best examined by considering the relationship between metabolic heat production (MHP or VO_2) and T_a. The $VO_2 - T_a$ relationship for the monk parakeet (Figure 5–25) illustrates the typical endothermic responses of mammals and birds to T_a. Metabolic heat production is high at low T_a to compensate for the high rate of heat loss. There is a range of T_a at which metabolic rate is minimal (basal metabolic rate, BMR) and constant; this is the thermoneutral zone. Metabolic rate increases at T_a below the lower critical temperature (T_{lc}) of the thermoneutral zone, and at T_a above the upper critical temperature (T_{uc}).

The relationship between VO_2 and T_a below T_{lc} generally conforms to a physical model for endothermic heat balance

$$VO_2 = C(T_b - T_a) \qquad (5.15)$$

where C is the thermal conductance (see Supplement 5–2, page 188). The relationship is not necessarily linear. The body temperature is not necessarily constant, but may decrease at lower T_a. Thermal conductance is not a physical constant, but can be varied by behavioral and physiological means. The wet thermal conductance (C_{wet}), which includes heat loss by evaporation, is not constant but increases at higher T_a as the evaporative water loss increases. The dry thermal conductance (C_{dry}) is less dependent on T_a than is C_{wet}, but it can also increase at high T_a (Figure 5–25) by physiological adjustments (e.g.,
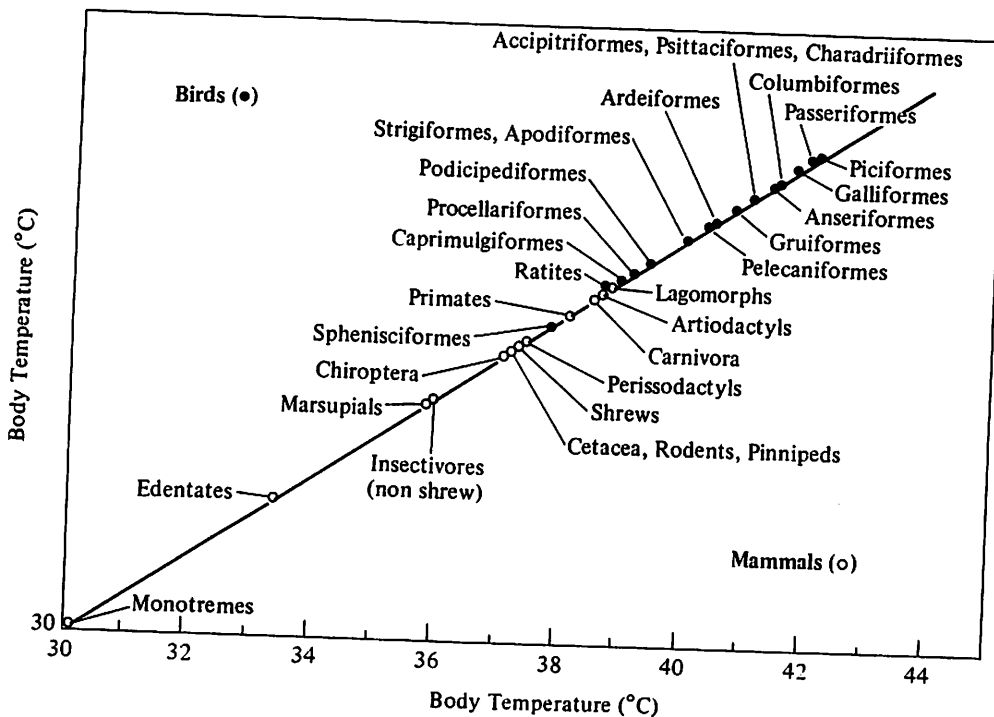

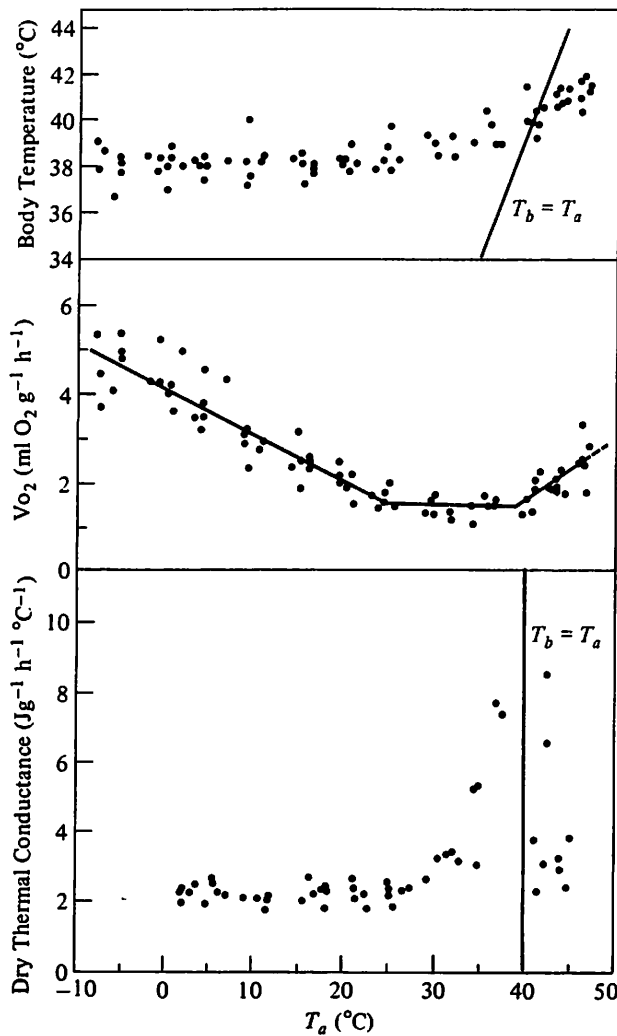**FIGURE 5–24** Average body temperatures for birds and mammals.

FIGURE 5-25 Metabolic rate (VO_2), body temperature (T_b), and dry thermal conductance (C_{dry}) as a function of air temperature (T_a) for the monk parakeet. *(From Weathers and Caccamise 1975.)*
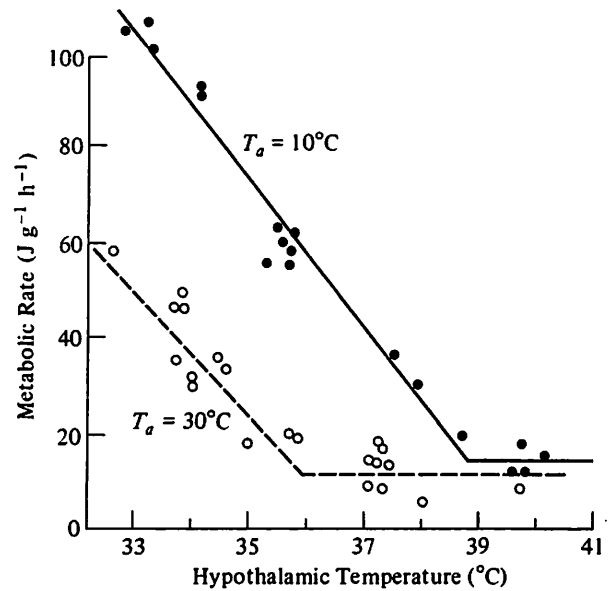

FIGURE 5-26 Metabolic heat production of a kangaroo rat, as a function of hypothalamic temperature, at two ambient temperatures. *(From Glotzbach and Heller 1975.)*

patterns of peripheral blood flow) and behavioral adjustments (e.g., posture). Finally, the relationship between VO_2 and $T_a(<T_{lc})$ often does not extrapolate to zero VO_2 at $T_a = T_b$; this is especially apparent for birds.

Most mammals and birds do not regulate T_b exactly constant over a range of T_a (e.g., Figure 5-25). The gain for thermoregulatory control systems is often about -4 to -8, and the thermoregulatory response is proportional to an error term (depends on $T_b - T_a$). We therefore should expect a slight (but significant) positive relationship between T_b and T_a for endotherms.

Body temperature is controlled primarily by hypothalamic and spinal cord thermoreceptors, with some input from peripheral thermoreceptors (see Chapter 2). The nature and extent of thermoregulatory responses (R; e.g., metabolic heat production, evaporative heat loss) are proportional to the difference between hypothalamic temperature (T_{hypo}) and the hypothalamic setpoint ($T_{b,set}$)

$$R = \alpha(T_{hypo} - T_{b,set}) \qquad (5.16)$$

where α is the proportionality constant for each thermoregulatory response for heat gain (α is negative) or heat loss (α is positive). For example, the metabolic heat production of the kangaroo rat *Dipodomys* has a hypothalamic setpoint of about $36°$ C and α is -10.83 J g^{-1} hr^{-1} $°C^{-1}$ at a T_a of $30°$ C; at T_a of $10°$ C the $T_{b,set}$ is about $39°$ C and α is -13.7 (Figure 5-26).

Adaptations to the Cold. Endothermic mammals and birds have essentially three strategies for surviving in the cold; they either decrease their rate of heat loss, increase their rate of heat production, or abandon thermoregulation of the normal T_b and allow it to decline (hypothermia, or torpor). Virtually all mammals and birds use the first two strategies, and some mammals and birds use the last