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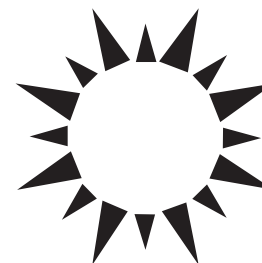
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A0005 *Thermoregulation*

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1. Introduction
 2. Mechanisms of Heat Exchange
 3. Managing Heat Flows
 4. Summary

Glossary

- G0005 **aestivation** Reducing energy expenditure below basal levels at very high ambient temperatures.
- G0010 **basal metabolic rate** The lowest metabolic rate reached by an animal maintaining bodily functions when at rest and not having recently eaten a meal.
- G0015 **behavioral thermoregulation** Behaviors that alter management of heat flows from outside to allow regulation of body temperature.
- G0020 **endothermy** Regulation of body temperature primarily using generation of heat internal to the animal.
- G0025 **euthermic** Precise regulation of body temperature around a set point in the approximate range of 35 to 45°C.
- G0030 **exothermy (ectothermy)** Regulation of body temperature using management of heat sources primarily external to the animal.
- G0035 **heliothermy** Thermoregulation primarily dependent on varying the interception of incoming solar radiation.
- G0040 **homeothermy (homiothermy)** An outmoded term describing the stability of body temperatures of endothermic animals; literally “constant temperatured.”
- G0045 **physiological thermoregulation** Physiological strategies that contribute to heat balance.
- G0050 **poikilothermy** An outmoded term describing the variations in body temperatures of exothermic animals; literally “variable temperatured.”
- P0005 Thermoregulation describes the process by which animals manage the flow of energy into and out of their bodies, with the aim of maintaining a relatively constant body temperature within a range of 2 to 3 K. Most vertebrate animals attempt to regulate their body temperatures within such relatively narrow limits because enzyme functions are strongly

dependent on temperature; therefore, there is only a narrow range of body temperatures within which metabolic processes can be optimized. Once body temperatures move outside these relatively narrow limits, animals start to experience profound reductions in their cellular functions and this has ramifications for their performance at the whole animal level. For many animals, exposure for even short periods to temperatures more than 10°C below or 5°C above those at which they routinely regulate their body temperatures is often fatal.

1. INTRODUCTION

S0005

The set points at which body temperatures are regulated vary tremendously among different animal groups. However, many animals regulate their body temperatures in the range of 30 to 45°C (303–318 K), and these animals are generally termed “euthermic.” Body temperature can be regulated by altering the flow of heat into and out of the animal (behavioral thermoregulation or exothermy) and by generating heat internally (endothermy). Different species vary in the extent to which they use these alternative strategies for regulating their body temperatures, and in most animals the strategies are combined to varying extents. However, the physical laws that govern the amounts of energy required under various circumstances are common to all animals, independent of how they ultimately meet these demands.

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2. MECHANISMS OF HEAT EXCHANGE

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All animate and inanimate objects exchange energy with their surroundings by four different mechanisms: radiation, convection, conduction, and evaporation. This section reviews the essential features

P0015

of these physical mechanisms in the context of their importance for animal heat balance.

1.0 (equal to the emissivity of a perfect emitting blackbody) and 0.0 (meaning the body would emit no radiation).

All objects emit amounts of radiation that are dependent on their surface temperatures and surface emissivities, and all objects also absorb radiation. Humans emit only in the infrared, and they absorb in both the infrared and visible spectral ranges. Objects that are good at emitting radiation at a certain wavelength are also good at absorbing it. Because the dominant sources of radiation are bimodally distributed with respect to their dominant wavelengths (i.e., in either the infrared or visible ranges), the capacity to absorb long- and shortwave radiation separately is often discussed. Longwave radiation emissivity/absorptivity tends to bear little relation to the color of the emitting surface as humans perceive it. Most animate objects have high water contents, and because water is a good emitter of longwave radiation, surface emissivities and absorptivities of most living organisms tend to be high (~ 0.95). However, absorption and reflection of shortwave radiation do vary with the color of the surface. Hence, dark colors have high absorptivities and light colors have low absorptivities. Capacities to absorb shortwave radiation are defined by the term “albedo.” This is a value between 0.0 and 1.0 that expresses the capacity of a surface to absorb shortwave radiation relative to a perfect whitebody reflector. Hence, an object with an albedo of 1.0 is a perfect reflector and absorbs minimal amounts of incident shortwave radiation, whereas an object with an albedo of 0.0 is a good absorber. People can directly experience the impact of variations in albedo on absorbed radiation amounts very easily by changing the color of their clothing and exposing themselves to bright sunlight. Few people will fail to recognize the advantages of wearing light-colored clothing on hot summer days. This trend of wearing light-colored clothing during summer is a behavioral thermoregulatory behavior.

An interesting question that puzzled researchers for a considerable period is why races of humans that originate in tropical areas have dark skin colors compared with races that come from areas in the temperate and arctic regions. Explanations of this difference often suggested that skin color was related to both long- and shortwave radiation and that, overall, the dark skin color was advantageous in hot conditions because on balance it absorbed less radiation. However, this explanation is incorrect. In fact, dark skin is not a thermoregulatory adaptation at all but rather is a response to increase

S0015 2.1 Radiation

P0020 All objects emit electromagnetic radiation. The emitted radiation can be characterized by two parameters: the wavelength of emitted radiation and its intensity. Emitted radiation has a characteristic distribution of wavelengths that depends on surface temperature of the emitting object. The distribution at any particular temperature is peaked with a positive skew. The wavelength of modal intensity varies as a function of the surface temperature. As objects get hotter, the wavelength of peak intensity of radiation they emit gets shorter. This inverse relationship is generally called Wien’s displacement law. Most objects on the surface of the earth have surface temperatures in the range of 253 to 313 K. The peak wavelengths of radiation emitted by objects in this temperature range are in the infrared. Because human eyes cannot detect infrared radiation, one cannot see the emitted radiation from most natural earth-bound objects directly. Glowing larva, molten metals, and hot coals in fires are notable exceptions of earth-bound objects that reach sufficiently high temperatures that the emitted radiation is directly visible by humans. Some animals have special sensory adaptations that enable them to detect infrared radiation. In particular, a group of snakes known as pit vipers can perceive emitted radiation from objects in the range of 273 to 313 K and use this to detect their prey. Because the prey thermoregulate, they are generally hotter than their surroundings and, thus, emit radiation with greater intensity and at higher wavelengths.

P0025 The other main source of radiation on earth comes from the sun. The surface temperature of the sun is approximately 6000 K. The wavelengths of radiation generated by objects at this temperature are between 400 and 700 nm. It is no coincidence that this is the range of wavelengths to which humans’ eyes are sensitive and which, therefore, is defined as the visible spectrum. When one sees “an object,” what one actually sees is the electromagnetic radiation that is reflected from its surface. The amount of energy that is radiated by a body depends on the surface temperature of the object and on whether it is a good or poor emitter of radiation. An object’s capacity to emit radiation is defined relative to that of a perfect emitter, which is called a blackbody emitter. Capacity of a surface to emit radiation is defined by a term called the emissivity (ϵ). Emissivities vary between

absorption of shortwave radiation before it can penetrate the skin and cause dangerous lesions to epithelial cell DNA. This means that dark races actually do absorb more shortwave radiation than do their light-skinned counterparts. However, the benefits of this absorption are illustrated by comparing the rates of skin cancers in aboriginal Australians, where skin cancer is virtually unknown, and white Australians, who have a broadly European heritage and where skin cancers occurred in nearly 3% of the population during the early 1990s until vigorous campaigns were started to encourage safe practices when out in the sun.

P0040 The intensity of emitted radiation is very strongly dependent on surface temperature. In fact, emitted radiation is proportional to the surface emissivity multiplied by the absolute surface temperature (K) raised to the fourth power. This scaling exponent of 4 is very important because it means that as objects get hotter, the amounts of emitted radiation become disproportionately large. Hence, the surface of the sun at 6000 K is only 20 times hotter than humans are, at approximately 300 K, but each square meter of the sun's surface emits 160,000 times more electromagnetic radiation than do humans. Of course, because of the inverse square law and the fact that the earth is 150 million km from the sun, the amounts intercepting our planet are very much diminished. The consequence of this is that shortwave solar radiation input and longwave radiation outputs of our bodies are of the same order of magnitude, with both being approximately 1 kW per square meter of surface

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S0020 2.2 Conduction

P0045 When any two solid objects are in direct physical contact, they exchange heat. Heat is "conducted" from the hotter object to the cooler object. The rate at which the heat flows depends on the surface area that is in contact between the bodies, properties of the material that connects them, and the path distance over which the heat is being conducted. The main property of an object that defines its capacity to conduct heat is called its thermal conductivity. Objects that conduct heat well are said to have high thermal conductivity, whereas those that conduct poorly are said to have low thermal conductivity. The inverse of conductivity is thermal insulation. Typical high-conductivity/low-insulation objects are metals and rocks, whereas typical low-conductivity/high-insulation materials are wood and fur. Among the lowest thermal conductivities of all is

that of still air. This is why natural and manmade insulative materials tend to consist of structures that aim to trap air and keep it stationary (e.g., expanded polystyrene). In fact, the thermal conductivity of fur exceeds that of still air, so if the fleece of a sheep is compressed (thereby reducing the amount of air trapped in it), the conductance of heat across the fur actually increases.

One might imagine that because most animals do not have large amounts of their surfaces in contact with other solid objects, the role of conductance in the process of heat exchange would be minimal. But although this is generally true, one area where understanding the principles of conductance is important is in understanding the flow of heat from the core of a body to its surface. Because animals consist of solid objects, the heat flows from the central core to the surface via conductance. To understand the flow of heat from an animal's core to the surrounding air, imagine that heat is produced centrally at a notional single point. The heat flows first through the tissues, carried partly by blood flow through the arterial and capillary network and partly by conduction through the cells and tissues themselves. In some animals, the heat must then flow through a barrier of fur or feathers, primarily by conduction through the hairs or feathers themselves but also by conduction through the trapped air, and finally dissipates from the thin boundary air layer overlying the outer surface of the fur, primarily by convection and the net loss of thermal radiation. Both the type of heat transport and the path length along which heat must travel determine the resistance that each layer offers to the flow of heat. Heat is transferred not only by conductance but also by convection due to movement of the blood, and the process of convection transfers heat much more rapidly than does the process of conduction. Thick layers of material with low conductivity by definition offer more resistance to heat flow than do thin layers. Because each layer offers a resistance to heat flow, temperature drops progressively between the core and the skin, through the fur, and finally into the surrounding air. The extent to which the temperature drops across a given layer is determined by the proportional contribution of that layer to the total resistance offered by all layers to the flow of heat. A thick and efficient fur or feather layer, which offers a high resistance to heat flow, will exhibit a large drop in temperature between its inner and outer surfaces, and the total flow of energy across it will be reduced. Conversely, the difference between the core of the body and the area under the skin may differ

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very little in temperature due to the high conductivity (assisted by convection effects).

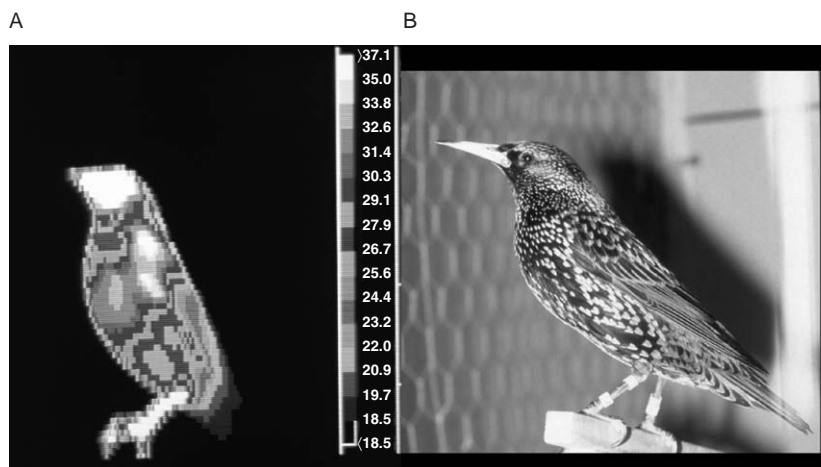
P0055 There are very strong parallels between thermal and electrical conductivity and the concepts of thermal insulation and electrical resistance. Concepts of electrical circuitry have been widely borrowed to help explain how heat flows within animals from core to periphery. In this context, it is useful to imagine the heat as though it were electricity flowing through a number of resistances that may be arranged in parallel within a given layer and in series between layers. The value of this approach is that it allows one to apply the same formulas that predict current and voltage in electrical circuits: $I = V/R_{\text{total}}$, where I is the current, V is the voltage potential, and R_{total} is the circuit resistance. When thinking in terms of heat rather than electricity, we simply substitute heat flow (H) for I , temperature gradient (ΔT°) for V , and the sum of the resistances in the various layers for R_{total} . Thus, the overall flow of heat away from the core is calculated by $H = \Delta T^\circ / R_{\text{total}}$, and because $R = 1/C$, this is the same as $H = \Delta T^\circ \cdot C$.

P0060 There are several benefits to thinking in terms of resistances and ΔT° . One is that the overall resistance (R_{total}) can simply be found from the sum of the equivalent resistances for each layer, remembering that an equivalent resistance refers to a single resistance that could replace two or more resistances in parallel. A second benefit is that the resistance offered by a given layer (x) can be calculated from

the heat flow and the temperature drop across that layer if the total heat flow is known ($R_x = \Delta T_x^\circ / H$). A third is that the relative importance of each layer in limiting heat flow is easy to visualize. Just as the voltage drop (ΔV_x) across a single resistor of a series can be predicted by the ratio of that resistor (R_x) to the total circuit resistance ($\Delta V_x = [R_x / R_{\text{total}}] \cdot V$), the temperature drop across a given layer is determined by the proportional contribution of the resistance in that layer to the total resistance offered by all layers ($\Delta T_x^\circ = [R_x / R_{\text{total}}] \cdot \Delta T^\circ$). Moreover, in this analogy, the total current (I) is equivalent to the total heat flux (H). Thus, factors that diminish I , such as elevated total resistance, can also be seen to parallel the effects of elevated total insulation on total heat requirement.

When peripheral blood flow is high due to dilation of the capillaries under the skin surface, considerable amounts of heat are transported to the skin surface by convective blood flow and the ratio of tissue resistance to the total resistance ($R_{\text{tissue}} / R_{\text{total}}$) is small. As a result, there is only a small temperature difference between core and skin, and the skin is seen as “hot.” The surface temperature depends on the thickness of the overlying insulative layer and, thus, the total resistance afforded to heat flow along any particular path. A thermal image of an animal that picks up the emitted radiation clearly shows this variation in surface temperature as a function of the thickness of the insulative layer and the resultant heat loss across this layer. Figure 1 shows a thermal

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F0005 **FIGURE 1** (A) Thermal image of a perching bird (a European starling, *Sturnus vulgaris*) and (B) a photograph of the same bird. In the first image (A), the camera detects the emitted longwave radiation and a computer uses the intensity of this radiation to generate, in real time, a false color map of the surface of the animal (see temperature scale at the side of the image). The second photographic image (B) relies on reflected shortwave radiation from the animal's surface. The surface temperature in panel A depends on the thickness of the external insulation layer. Areas where the layer is thinnest, particularly the head and legs, have the highest temperatures and the greatest flux of heat energy

image of a perching bird illustrating that the hottest areas are the legs and the face where the feathers are either absent or thin. The coolest areas are where the wings add an extra layer of insulation over the animal's lateral and ventral surfaces. Understanding this regional variation in surface temperature provides clear insight into why roosting birds often tuck their heads down under their wings and pull one leg up into their ventral plumage. By doing so, the birds conceal the hot parts of their bodies under layers of insulation and, thus, reduce the total heat flux. This is another form of behavioral thermoregulation.

P0070 Clearly, if the skin surface is hot due to dilation of the capillaries, another mechanism that animals might use to conserve heat is to reduce the flow of blood to the surface by closing down these capillaries, that is, vasoconstriction. In these conditions, convective heat transport to the skin declines toward zero. Most of the tissue resistance is now determined by the slower conduction of heat through the tissue matrix. The skin is seen as "cool" due to this increase in tissue resistance, resulting in a higher $R_{\text{tissue}}/R_{\text{total}}$ ratio. As a result, less heat is delivered to the base of the fur, ΔT° through the fur is smaller, and heat flow through the fur is reduced.

P0075 The ability to depress skin temperature by vasoconstriction is affected by body size. By definition, small animals have short path lengths between the organs (where much of body heat is produced) and the skin surface, whereas large animals necessarily have longer path lengths. As a result, small animals have relatively low tissue resistance, and hence high skin temperatures, compared with those of large animals. This effect may be enhanced not only by constricting the blood supply to the surface but also by covering the undersurface of the skin with a layer of fat or blubber. Fat has a lower thermal conductivity than does lean tissue and, hence, acts as a barrier to heat flow. The best-known examples of this are the aquatic seals and whales that rely on a thick layer of subcutaneous blubber as insulation. Many terrestrial hibernating mammals also lay down substantial subcutaneous fat deposits. Although fat in these hibernating animals serves primarily as a means of energy storage, by analogy with aquatic mammals, one might be led to think that fat could also have a secondary role as an insulation layer for terrestrial animals. To analyze this problem, one should imagine a small lean animal with a tissue path length of 4 mm and a fur thickness of 6 mm and then consider what effect the deposition of a 1-mm thick subcutaneous fat deposit would have on heat flow. Muscle, fat, and fur offer resistances to heat flow of

approximately 21.7, 46.9, and 262.9 $(\text{W}/^\circ\text{C}/\text{mm})^{-1}$, respectively. For a lean animal having no fat deposit, the tissue resistance is $4 \text{ mm} \cdot 21.7 (\text{W}/^\circ\text{C}/\text{mm})^{-1}$, the fur resistance is $6 \text{ mm} \cdot 262.9 (\text{W}/^\circ\text{C}/\text{mm})^{-1}$, and the overall resistance is the sum of the two or 1664.2 $(\text{W}/^\circ\text{C})^{-1}$. Adding a 1-mm subcutaneous fat layer would increase the overall resistance by $1 \text{ mm} \cdot 46.9 (\text{W}/^\circ\text{C}/\text{mm})^{-1}$, raising the overall resistance to 1711.1 $(\text{W}/^\circ\text{C})^{-1}$, only 2.8% higher than the lean condition. Thus, the fat layer would reduce heat flow by only 2.8%. Therefore, we can conclude that 1 mm of fat is not an effective barrier to heat loss for small terrestrial animals and that fat storage in hibernators and other small animals probably does not serve as an insulator.

2.3 Convection

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P0080 Conduction of heat occurs when two solids of different temperature are in contact. Convection occurs when a solid is in contact with a fluid (generally air or water on Earth) of different temperature. The "different temperature" part of this definition is often neglected, but it is clear that energy can only flow down a thermal gradient, so if there is no temperature differential the heat flow will similarly disappear. Using a fan increases airflow across the surface of the face, and because this is naked skin that is well perfused with blood, the increase in convective heat flow is an effective way in which to contribute behaviorally to thermoregulation by elevating surface heat losses. However, there is an increase in endogenous heat production when using a fan due to the muscular activity involved in the waving motion. Once air temperature rises to the same level as skin temperature, heat losses fall to zero no matter how hard one fans. The heat generated by fanning exceeds that from cooling under these conditions.

P0085 In fact, the heat loss by convection is a function of several factors. One is the driving temperature gradient, that is, the difference in temperature between the solid and the fluid in which it is immersed. The area over which heat is being lost is obviously important, and the shape and structure of the surface also affect how exposed it is to the fluid flow and, hence, the magnitude of the impact of the velocity of flow. The conductivity of the fluid is also an important factor. For example, water has a conductivity 23 times greater than that of air, and this greatly magnifies the cooling effect of convection in water. Although velocity is a factor in heat loss by convection, there is still some loss when an object is

stationary and there is no external flow of the fluid. This is a state called free convection. Free convection occurs because the air close to the surface of an object becomes heated by the object itself, and as this air warms up, its density declines and it rises upward. Standing humans in a completely still condition have plumes of hot air rising off the tops of their heads, and this hot air is replaced by colder air coming in from below. Therefore, convection currents are generated by the existence of a hot object within a cool liquid. But clearly, as the fluid moves as a whole, the velocity of that flow influences the convective heat loss. This is a state of forced convection.

P0090 The interaction between surface characteristics and velocity of flow on forced convective heat loss is complex. However, the relationship between airflow and heat loss generally follows a nonlinear pattern of diminishing increase with increasing velocity until at some point further elevations in velocity have only marginal effects. The exact exponent to which velocity is raised in these relationships varies somewhat with the shape and surface structures on the object, but a commonly assumed exponent is 0.5. Thus, heat loss increases as a function of the square root of fluid velocity. This is because the surface insulation is provided primarily by the thin skin of still air at the body surface known as the boundary layer. This air is gradually stripped away as velocity increases, but eventually when it has all gone, there is nothing else to lose. The manner in which the boundary layer is stripped depends on how the flow transits from laminar to turbulent flow, and characteristics of the shape and surface can influence this transitional velocity, thereby complicating the exact value of the exponent. It is clear that animals can use these properties to minimize convective heat loss by altering their shape to promote laminar flows. The example cited earlier of birds tucking their heads under their wings and standing on one leg may also function to present an aerodynamically favorable perspective in an airflow to minimize turbulent airflow and, thus, minimize convective heat loss.

S0030 2.4 Evaporation

P0095 The previous three modes of heat flow all work down temperature gradients. Heat flows from hot objects to cold objects by the processes of radiation, conduction, and convection. However, evaporation allows an object to lose heat even if the surrounding medium in which it is immersed is hotter than the object itself. This is consequently an essential thermoregulatory mechanism for many animals

because it is the only method they can employ to keep cool if ambient temperatures exceed their body temperatures. Evaporation involves using energy to convert liquid water into the gaseous phase. Because water is strongly hydrogen bonded, the amount of energy required to convert liquid water to gas is high and, thus, evaporation is a very effective method for cooling down. To achieve this, many animals have specialized mechanisms such as sweating (where water oozes onto the surface of the animal and evaporates from there), panting (where a respiratory airflow is passed over the tongue to promote evaporative losses), and self-anointing (where the animal licks itself and the evaporating saliva provides the cooling). The capacity for evaporation depends on the ability of the surrounding medium to accept water vapor. The capacity of air to hold water vapor increases as a function of temperature. When the air is saturated, it is said to have a relative humidity of 100%. At this point, the air can accept no further water vapor and net evaporation from the surface of an object in that air ceases. This is why humid conditions are far more uncomfortable for humans than are dry conditions, even though in the latter case it may be hotter in absolute temperature. In dry conditions, one can thermoregulate by evaporation, but when the conditions also include very high humidity, even this avenue for heat loss is shut down.

3. MANAGING HEAT FLOWS

For very small animals (less than 1 mg), their surface areas are such that sustaining any temperature differential between the inside of the animal and the environment is nearly impossible. These animals maintain a constant internal temperature only by locating themselves in an environment where the temperature itself is constant. If the environment fluctuates in temperature, the animals have mechanisms to avoid the most extreme conditions in suspended states until the conditions improve again. Most lower invertebrates approach the problem of thermoregulation in this manner, that is, by avoidance. However, once animals become larger, their relative surface areas decline and it becomes feasible to sustain a temperature differential between the inside and outside of their bodies. This means that the animals can maintain homeostasis of their internal temperatures despite the range of external conditions and the variability in internal heat production as a by-product of activity. Most larger invertebrates have some limited capacities to regulate

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their temperatures to some extent, and they combine these capacities with physiological or actual physical avoidance to survive temperature extremes.

P0105 However, it is in the vertebrates that thermoregulation has evolved to its greatest diversity and sophistication. The remainder of this article discusses the thermoregulatory strategies adopted by the major vertebrate groups.

S0040 3.1 Fish

P0110 Most fish spend most of their lives in water. This lifestyle simplifies the consideration of heat fluxes because it is not possible to engage in evaporation underwater, and beyond only a few meters of depth nearly all radiation has been absorbed. Thus, the heat budget management of fish is more simplified than that of terrestrial vertebrates. Water has a high specific heat capacity and, hence, tends to buffer environmental extremes. For example, the surface temperature of the Pacific Ocean differs by approximately 5 K over a distance of several thousand kilometers. The same temperature difference on land can be found between the shaded and exposed sides of a tree, that is, over a distance of a few meters. Therefore, fish are generally in a medium where the external temperature is relatively stable. The key problem, then, is that because of variations in activity, as well as variations in the energy required to digest food, the rates of endogenous heat production by the animals fluctuate widely. Because the external temperature is relatively constant, the driving gradient for heat loss by convection would also appear to be constant. Therefore, one might anticipate that as fish become active, they may experience thermoregulatory problems dissipating their body heat.

P0115 However, in addition to having high thermal conductivity relative to air, water has a low oxygen content relative to air. In fact, even oxygen-saturated water has only 1/40th the oxygen content of atmospheric air. Therefore, fish need extremely efficient mechanisms to extract oxygen from their environment to support their metabolism. The main mechanism they use is a countercurrent exchange mechanism in the gill arches, which have highly specialized enlarged surfaces to facilitate oxygen uptake and the removal of carbon dioxide generated by oxidative metabolic processes. What is a good mechanism for extracting oxygen from water is also a very efficient mechanism for getting rid of body heat. Indeed, because water has 23 times the cooling power of air yet only 1/40th the oxygen content, for

each milliliter of oxygen extracted, the cooling power available to fish is approximately $23 \times 40 = 920$ times greater. Fortunately, elevated oxygen requirements occur when the animals are active and generating the most heat. So, there is an automatic passive feedback system that keeps the body temperatures of fish at the same level as their environment regardless of their level of activity. When activity increases accompanied by an increase in heat production, increased ventilation of the gills to get oxygen to support the activity automatically dumps the excess heat, avoiding overheating.

This is a workable strategy so long as the environmental temperature remains stable. However, temperatures vary spatially in bodies of water, particularly if the water is shallow and able to be heated by the sun in places but shaded elsewhere. Moreover, most bodies of water develop thermal stratification where the upper layers are heated by solar radiation effects but there is an abrupt thermocline separating this surface-heated water from the more stable cold water at depth. Obviously, fish might swim into such cool areas or into hot areas, with potentially serious consequences for their body temperatures. Fish accommodate such spatial temperature effects by behavioral strategies. They swim faster and turn more as they move into water that is cooler or hotter than their preferred temperature, and these simple kinetic mechanisms bring the animals back to an environment with a water temperature they prefer. However, if rapid temperature changes occur across an entire area, the animals have no mechanisms to avert disaster. Anyone who has kept tropical fish and had a heater fail in the tank in a cold temperate environment likely has observed the inability of fish to survive such an event. In the wild, these situations must be very rare. However, seasonal shifts in the temperature of the environment are commonplace, and fish have evolved a series of complex behavioral and physiological responses to overcome such seasonal effects.

In fact, a common strategy in the face of the change is simply to avoid it by migrating, and many fish species do this in the ocean. However, in freshwater lakes where the whole available environment is heating or cooling, migration is often not an option. As water cools down, the problem facing the fish is that their cellular performance, and hence metabolic and ultimately whole body performance, might be compromised. The issue then is to sustain cellular processes functioning at the lower temperature. To achieve this, fish alter the amounts of enzymes they manufacture, shift production to

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isozymes that work best at lower temperatures, and modulate the medium in which the enzymes are working to maximize their activities. These have been called the quantitative, qualitative, and modulative responses, respectively, and together they comprise the physiological thermoregulatory strategy that allows fish in seasonally changing environments to survive without running away.

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However, some fish do not conform to this pattern of thermoregulatory control. This group includes tuna, swordfish, and large game fish such as marlin. In these animals, there is a complex countercurrent heat exchange blood flow that reclaims heat from the blood before it passes through the gills. Hence, blood at the gills is at water temperature, and blood in the core body can be up to 15 K warmer. This allows these animals considerable flexibility to sustain performance in waters of varying temperature, and they use this capacity to swim below the thermocline into cooler waters and exploit prey populations living there.

S0045 3.2 Reptiles

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Most reptiles live on land. Therefore, the problems they face include those faced by fish of highly variable rates of endogenous heat production when the animals are physically active or digesting food. But combined with this problem is the fact that the environment in which reptiles often find themselves contains a tremendous spatial matrix of conditions where potential heat flux varies over orders of magnitude. Moreover, the modes by which heat flows between the animals and their environment entails a level of complexity way above that experienced by the average fish because radiation, evaporation, and conduction all come into play in addition to convection. Therefore, as might be anticipated, reptiles have extremely sophisticated thermoregulatory capacities to sustain their bodies at relatively constant temperatures in the face of this potential heat management nightmare.

P0140

This seems so obvious that it may come as a surprise to find that for a long time the thermoregulatory capacities of reptiles were considered extremely rudimentary. These impressions came from observations made during the 1800s of animals that had been captured in the wild. The typical reptile was captured from the wild and held overnight in a box, as was frequently the practice for animal collectors. When the reptile was removed from the box the next morning (assuming that the animal was not unduly large), it would generally

have reached thermal equilibrium with its surroundings and have a body temperature similar to that of the box. If it was cold, the body temperature would also be cold and the animal would have the consequent impacts of reduced body temperature on performance, including extremely sluggish movements and a generalized inability to respond to stimuli. Therefore, it is a small wonder that the animals were termed “cold-blooded” or poikilothermic (literally “variable temperatured”), reflecting the notion that they were incapable of thermoregulation and, thus, that their body temperatures varied along with the many temperatures of the environment. One of the few physiological skills the animals appeared to have was the ability to survive body temperature fluctuations that would be lethal to most mammals.

This notion arose from the abstraction of these animals from their environment. When a pioneering group of physiologists during the 1950s started to examine animals in the wild, they uncovered the true nature of reptilian thermoregulatory capacities. In fact, during the daytime, most reptiles are very good at regulating their body temperatures within very narrow limits. They do this primarily by regulating the level of absorption of shortwave radiation. To increase body temperature, reptiles bask in the sun. They maximize uptake of absorption by exposing the maximal area they can toward the sun, adopting body angles that maximize interception of radiation. Many reptiles have specialized dark patches on their surfaces that serve to decrease surface albedo and, thus, absorb more incident shortwave radiation, not unlike little thermal windows on their surfaces. By locating themselves onto hot surfaces that have heated up in the sun, they can gain additional energy to heat themselves by conduction. To cool down, the animals turn themselves away from the sun, minimizing their interception area and turn their dark patches away so that they no longer absorb. If the problem is severe, they seek shaded areas where the incoming shortwave radiation is massively reduced and the substrate in which they are in heat exchange by conduction is cooler. Ultimately, animals may avoid the environmental extremes by burying themselves, either under rocks or in the substrate itself.

P0145

The dependence of reptiles on shortwave radiation from outside their bodies to control their energy balance, and hence their body temperatures, has been termed “heliothermy” (from *helios* or “the sun”). However, a more common term emphasizing the fact that most of the heat used to control body temperature is from external sources is “exothermy” or “ectothermy.” One disadvantage of relying so

P0150

heavily on the solar radiation for energy is that once the sun goes away, the animals are deprived of their primary heat source and start to cool down. This is why reptiles left in boxes overnight generally have body temperatures in the morning that are at the same temperature as the ambient temperature and, thus, appear to be unable to thermoregulate. This thermal dependency is mitigated somewhat by size given that larger animals, by virtue of their greater surface/volume ratio, cool more slowly. For example, komodo dragons, which are the largest extant lizards, spend all day at body temperatures of roughly 36 to 38°C but overnight cool by only 5 to 8°C, even when the environmental temperature is approximately 20 to 25°C. This slow cooling is primarily a function of their large size. The heavy dependence on the sun also explains why the distribution of reptile species is primarily tropical.

P0155 Problems arise for reptiles if they require going into water. Because of the very high thermal conductivity of water, combined with the fact the animals are cut off from their usual source of external radiation, reptiles in water cool rapidly to the water temperature. Marine iguanas from the Galapagos Islands routinely feed in the splash zone at the top end of beaches and may dive to feed on algae up to 3 m deep, spending protracted periods submerged. That these animals can submerge for long periods without succumbing fatally has been known for some considerable time. Darwin, in *The Origin of Species*, remarked on a rather crude experiment performed by a sailor in which a marine iguana was tethered to rocks and submerged for an hour but was still alive on recovery. Studies of blood circulation have shown that marine iguanas have exquisite control over their circulatory systems, allowing them to vasoconstrict during diving to concentrate blood flow in their core and, thus, retard total heat loss and their cooling rate, but then to vasodilate on emergence to rapidly heat up by a combination of basking (uptake of solar radiation) and direct contact with the black lava rocks that form the beachheads (conduction). Studies of other marine reptiles such as sea turtles indicate that similar circulatory adjustments allow them to minimize cooling and/or maximize heating rates by adjusting blood flow into their front flippers as they encounter waters of varying temperatures. Leatherback turtles might even have some degree of endothermic heat production beyond the slow cooling engendered by their large size, allowing them to stray outside tropical waters, but this capacity is a matter of some debate.

However, other reptiles certainly do have the capacity to generate heat internally. Probably the best example of this is brooding pythons. These large snakes are able to generate heat internally, allowing them to transfer heat to their eggs and thereby stabilize incubation temperatures. The mechanisms involved in this internal heat production appear to include only shivering, that is, systematic contraction of the skeletal muscles not linked to gross body movement that generates heat as a by-product. However, even in these large snakes, the amounts of heat generated are insufficient to enable the animals to maintain a constant high body temperature in the face of declining ambient temperature when there is no external source of radiation. P0160

3.3 Birds and Mammals

S0050

If a bird or mammal is placed overnight in a box, and the animal is deprived of an external source of heat but is provided with food, in the morning its body temperature will be largely independent of the ambient temperature. This contrasting observation to the response of reptiles led early researchers to classify these animals as “homeotherms” (literally “same temperature”), reflecting the stability in the body temperatures, and to assume that these animals have much more sophisticated systems of thermoregulation. In fact, the problems faced by birds, mammals, and reptiles are very similar—enormous changes in the driving gradients combined with great variability in the endogenous heat production due to exercise. P0165

However, the solution to the problem that has evolved in birds and mammals is radically different. This does not mean that birds and mammals do not take advantage of the ability to manage their heat flows in behavioral exothermic ways. Many birds and mammals bask in the early morning sun, using exogenous shortwave radiation to raise their body temperatures. Both groups seek shade to avoid overheating, husky dogs prostrate themselves on snow to cool down after running, and nearly all birds and mammals exhibit a large number of other minor behavioral adjustments to manage their heat budgets (some of which were mentioned previously in the context of describing the modes of heat transfer). But the main difference is that whereas nearly all of the heat used by reptiles is externally derived, for mammals and birds it is internally derived. Hence, these animals are often called “endotherms.” Functionally, both birds and mammals are endothermic, but the physiological mechanisms they use to P0170

generate the heat are radically different; birds use shivering, whereas mammals have evolved a specialized tissue (called brown adipose tissue) that serves to generate heat.

P0175 To understand the variations in the energy demands of endothermy, it is useful to consider the energy that would be required to sustain the temperature of a beaker of water that nominally represents an animal's body. If one had a beaker of warm water at, say, 38°C and it was standing in an environment of 20°C, it would cool down by the processes of free convection, net radiation losses, and conduction to the surface on which it was standing. Therefore, to keep the water hot, one would need to place a heater in it and deliver sufficient energy internally to balance these heat losses. Because radiation, convection, and conduction all are functions of temperature difference between the beaker and the environment, the amount of energy one would need to supply with the heater would be a linear function of ambient temperature, crossing the x axis at the temperature of water in the beaker (Fig. 2A). That is, the energy one would need to supply if the ambient temperature was 38°C would obviously be zero because the beaker at 38°C would already be in thermal equilibrium. The gradient of the relation between heat requirement and temperature is termed the "thermal conductance" of the system under consideration. The gradient of this line reflects how efficiently the body exchanges heat with its environment. Hence, one could reduce heat flow and, hence, the heat requirement by wrapping the beaker in a blanket. The more insulation layers one added, the shallower and shallower the gradient would become as thermal conductance declined.

P0180 In the imaginary system just described, the minimal heat requirement to sustain the beaker temperature is zero. However, real animals cannot have zero heat production. This is because everything they do requires energy. Even when an animal is completely stationary, all its cellular metabolic processes still generate heat as a by-product. If we cross the lines of thermal conductance with this minimal heat production, it becomes clear that these lines intersect at certain points. These are the ambient temperatures where the animal's minimal heat production exactly balances its heat requirement from its thermal conductivity. Above this temperature, the animal is producing too much heat, and below this temperature, it is not producing enough heat to maintain energy balance. This point is called the lower critical temperature for an endotherm. Lower critical temperatures are lower

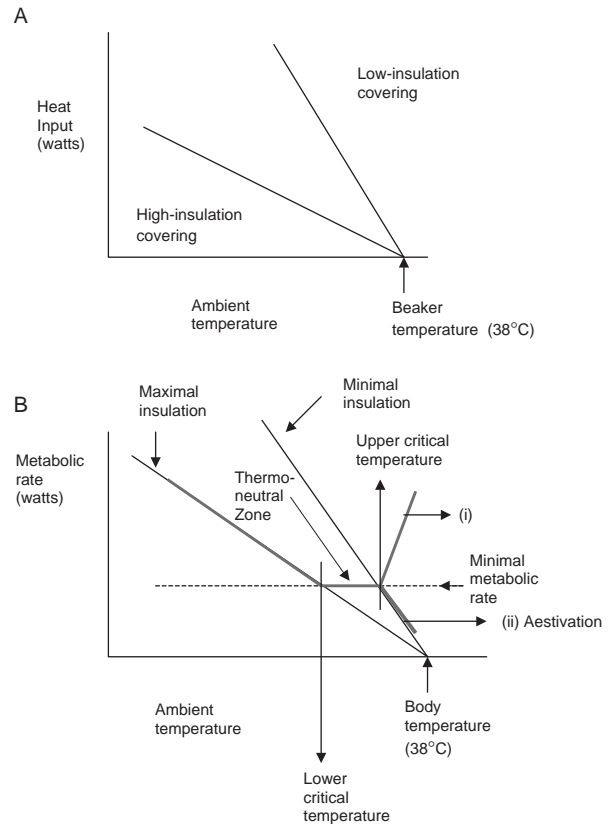


FIGURE 2 (A) Heat input required to sustain a beaker of water at a constant fixed temperature of 38°C as a function of ambient temperature and the thermal conductance of the material surrounding the beaker. Lower thermal conductance (higher insulation) leads to lower energy demands. When the environmental temperature equals 38°C, the heat requirement falls to zero. (B) Pattern of heat requirement as a function of ambient temperature and thermal conductance, with the minimal metabolic rate of an animal overlaid on this pattern. Where the minimal heat production crosses the minimal thermal conductance is called the lower critical temperature point. At lower ambient temperatures, an endothermic animal must supply heat internally to remain at the same body temperature. Above the lower critical temperature, metabolism remains constant (thermo-neutral zone) and animals modulate their thermal conductance until they reach their maximal thermal conductance (lowest insulation) at the upper critical temperature point. Above this point, animals can recruit mechanisms to dissipate heat but paradoxically raise their heat production to do this (i), or they can start to shut down their minimal processes and aestivate (ii).

F0010

in animals with lower thermal conductances. At temperatures below the lower critical point, an animal must elevate its endogenous heat production to balance heat losses if it is to sustain its body temperatures. The exact requirements track along the line defined by the thermal conductance. Above the lower critical point, the problem an animal faces is to get rid of the surplus heat. It can do this by

making behavioral adjustments that increase thermal conductance (e.g., adopting postures that facilitate airflow, reducing radiation uptake by seeking shade). Humans are uniquely able to rapidly manipulate their external insulation levels by taking off their outer clothing.

P0185 It is possible, in making these behavioral adjustments, to elevate conductance so that the minimal heat production balances the heat loss. However, at some point, these behavioral mechanisms can achieve no greater increase in conductance. When ambient temperatures rise above this point, the animal has to do something different. This point is called the upper critical temperature. Between the lower and upper critical temperatures of an endotherm, metabolic heat production remains constant and independent of temperature. This zone is called the thermoneutral zone. It is bounded by the upper and lower limits of variation in an animal's thermal conductance. If temperature rises above the upper critical point, an animal can do one of two things. First, to balance heat production with heat requirement, it can start to shut down its basic metabolic processes and fall into a state of lethargy that is called aestivation. Second, it can spend a little energy, paradoxically increasing heat production, if the net heat loss by this procedure is increased. In general, these mechanisms involve increasing evaporative water loss. When temperatures continue to rise, this increase gets exponentially steeper as the animal brings into play increasingly desperate measures to stay cool. Obviously, at some point, water loss in these states becomes a critical factor, and eventually the animal cannot regulate temperature any longer and the body temperature starts to rise—perhaps fatally if water cannot be replenished.

P0190 This model of heat loss in endothermic animals is generally called the “Newtonian cooling model,” and although it involves several simplifications of the actual situation observed in many animals, the model highlights some of the features of being endothermic and how these differ critically from those of exothermic animals. First, examination of the gradients of the curves relating thermal conductance to energy requirements clearly shows that the greater the degree of external insulation, the lower the energy demands of endothermy. Therefore, simple power demand arguments suggest that as the temperatures get cooler, endothermic animals should thicken up their external insulation layers. Indeed, many examples of this are observed in nature; Tropical endotherms generally have much less external insulation than do temperate and arctic

equivalents, and temperate and arctic animals often molt their external insulation seasonally between a thick winter coat and a thin summer coat. Indeed, humans also make the same seasonal and latitudinal alterations in their external insulation and may make such modulations over much shorter time scales of minutes as the heat requirements change.

What is perhaps less obvious is that the surface/ volume ratio effects mean that larger animals also have lower thermal conductances and lower requirements to balance heat loss (per gram of body tissue). Therefore, a power argument suggests that it is advantageous for animals in cold conditions to be larger than their conspecifics in warmer climates. This is known as “Bergmann's law” and has a corollary, “Allen's rule,” that not only should animals get larger in colder climates, but their appendages should get smaller as well so as to minimize heat losses. There are many examples of animals conforming to Bergmann's law, but as many endotherms do not conform to it as do, and many species actually show converse trends. Moreover, many exotherms show similar trends despite the energetics arguments not applying to them. This illustrates that power arguments and surface/volume ratios are but one of many selective pressures on animal body size, making generalizable rules difficult to formulate.

P0200 As animals get very large, they start to face the problem that their thermal conductance curves are so shallow that they are nearly always below the minimal metabolism line. These animals face problems in dissipating heat; consequently, to facilitate this process, they reduce the extent of their external insulation. Indeed, the largest extant land mammals, elephants and rhinos, have dispensed with external insulative fur completely. However, for most endothermic animals, the main problem they face is keeping heat they generate internally inside their bodies, and that is why nearly all of the endothermic birds and mammals have well-developed fur or feathers. This contrasts with the situation in reptiles that have no external insulation at all. External insulation layers would clearly be detrimental to reptiles, whose major source of heat is external, because the insulation would retard the heat from getting in. An obvious and seemingly paradoxical exception to the external insulation rule are the marine mammals. This is paradoxical because if one group of animals might be expected to most need external insulation, it would be endotherms immersed in water—with their thermal conductivity 23 times greater than that of air. Why have these animals not evolved or lost their fur? The answer is

that fur is not hydrodynamic given that its major function is to trap a layer of air. By replacing the external fur with an internal blubber layer, many marine mammals have overcome the problem that the fur layer would interfere with their abilities to swim and perform in the aquatic environment. It was shown earlier that fat layers are ineffective as insulation for smaller mammals. Similarly, smaller aquatic animals, such as sea otters, mink, and water shrews, retain their fur despite its unfavorable hydrodynamic properties.

P0205 Endothermy clearly has many advantages in freeing endothermic animals from the dependency on solar radiation. Endotherms can use solar radiation if they wish (somewhat less efficiently due to their external insulation), but if the sun does not shine, they are still able to function effectively, unlike their exothermic relatives. The main disadvantage of being endothermic is that because the energy for heat generation comes from within, the animals must find and eat considerably more food to fuel that energy requirement. Estimates made on small birds and small reptiles of their total daily food requirements suggest that small endothermic birds may, in fact, need to eat 50 to 100 times more food daily than do small lizards of equal body mass.

S0055 3.5 Dinosaurs

P0210 The question of whether the dinosaurs were endotherms or had thermoregulatory strategies similar to the modern exothermic reptiles to which they were more closely related has been an issue of debate for more than 100 years and, in fact, dates back to the very first discoveries of dinosaur fossils. Wilfred Owen, who gave the group the name “Dinosauria,” actually suggested they were probably warm-blooded animals, but this appears to have been more of a political statement to attempt to refute Darwinism than a truly held belief. Throughout the first half of the 20th century, it was mostly believed that dinosaurs were exotherms. However, opinion started to turn during the late 1960s and early 1970s, particularly due to the work of Robert Bakker and publication of his book, *The Dinosaur Heresies*, in 1977. By the late 1990s the public perception of dinosaurs had certainly embraced the idea that they were endotherms.

P0215 Several lines of evidence point toward this conclusion. However, many other lines of evidence paint a more confused picture. For example, although we might not expect the larger dinosaur representatives to have external insulation, we would

certainly expect this for the smaller representatives. Yet, apart from an indication of some feathering on recent fossils from China, all other small dinosaurs appear to have been devoid of external insulation. In contrast, there is clear evidence that another group of reptiles, the Pterosaurs, appear to have been endothermic, supporting their capacity to fly, and also had external insulation in the form of fur on their bodies. Moreover, extant endotherms have bony structures in their nasal passages that support structures to reclaim heat from respiratory gas exchange, that is, turbinates. All extant endotherms have these bony structures, but they are absent in fossil dinosaurs. Overall, then, the evidence supporting an endothermic dinosaur thermoregulatory strategy is at best confused.

4. SUMMARY

S0060

Thermoregulation is the maintenance of a stable body temperature by managing the flow of heat into and out of the body. Although there are two major strategies, exothermy (relying on external heat sources) and endothermy (relying on internally generated heat), all animals use a combination of behavioral and physiological strategies to control their heat balances to some extent. In fish, amphibia, and reptiles, the balance is much more toward exothermic regulation, whereas in mammals and birds, the balance is shifted toward endothermy. The jury is still out on the thermoregulatory strategies used by the extinct dinosaurs, although one ancient extinct reptilian group whose members were contemporaries of dinosaurs, the Pterosaurs, were almost certainly endotherms.

P0220

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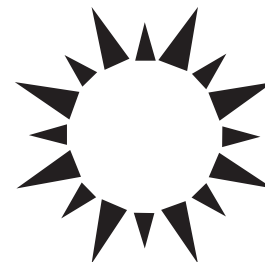
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