**Abstract**

As researchers, teachers, and practitioners we often encounter young professionals and lay adults who do not understand basics of mammalian body temperature regulation. Often their single solid piece of knowledge is that some vertebrates (mammals and birds) are warm-blooded and some (fish, amphibians, and reptile) are cold-blooded, which is incorrect. There are many thermal capabilities and regulatory strategies. We provide basics of body temperature regulation, including definitions, its evolution, examples of body temperature variability, unique examples of hibernation and torpor, and we explain how a better understanding benefits individuals in personal and professional lives. We suggest a simple replacement of the warm-blooded paradigm that can be used to inform even young students. As a starting point, students young and old are familiar with species of mammals (e.g., platypus and opossums) that do not maintain as constant or as warm of a body temperature as humans and dogs. Students also know that humans do not maintain a constant body temperature over time (they have a “temperature” when sick) or all part of their body (they have cold hands and feet outside in winter).

**Key Words:** warm-blooded; endotherm; heterotherm; hibernation; homeotherm; heterotherm; mammal; torpor.

**Introduction**

Young students learn three to five characteristics that define fish, amphibians, reptiles, birds, and mammals. Mammals are warm-blooded, nourish young with milk from mammary glands, and possess hair and a four-chambered heart—accompanied by “humans are mammals.” A few anomalies are noted: whales do not have much hair, and the duck-billed platypus is an odd mammal that lays eggs. It makes sense that third-graders learn a few relatively simple characteristics. Unfortunately, those limited characteristics remain the life-long definition of mammals for a large part of the population. We routinely interact with well-educated people that retain the simple definition that mammals are warm-blooded. They have added facts like which species are good for milk, meat, fur, and as pets, and that bats and bears hibernate, but being warm-blooded remains central to their definition.

As researchers, teachers, and practitioners we find this disheartening because it is not just misleading, it’s wrong. A recent internet search for “warm blooded animals” produced 7,140,000 results, and at the top were sites for kids. How do you compete with that? We hope small changes to information provided during early learning will help change the understanding of temperature regulation in mammals and correct the long-standing warm-blooded myth. It is not our intent to make the reader a thermal biologist, but we provide information for basic understanding of mammalian thermoregulation. We keep jargon to a minimum but include key terms integral to understanding and teaching about mammalian body temperature.

We explain why the term warm-blooded, even as short-hand for “a constant body temperature,” is inaccurate. We address persistent systemic anthropocentric myths, like comparing and valuing thermoregulatory capabilities against those of humans: a variable body temperature is not an evolutionary failure, nor is a constant body temperature necessarily “good, better, or advanced.” We provide examples we find interesting and hope will help engage students. We take a quick look at the evolution of thermoregulation because we think it is helpful to know, and we hope it will help capture students’ interest. We look at the special instances of hibernation and torpor. Finally, we point out how a paradigm shift will benefit individuals in their personal lives, while watching TV or birds, or making personal and professional decisions about conservation and perhaps even climate change.

The paradigm shift is simple: a warm- versus cold-blooded dichotomy misrepresents organismal thermoregulation. Evolution
does not produce a one-size-fits-all solution to a complex problem like staying warm, or cool, in a diversity of variable environments. “Cold-blooded” animals do not just passively warm and cool, and “warm-blooded” mammals and birds use a continuum of thermal controls ranging from environmental conformance to strictly maintained body temperatures. There is no single standard, but we expect nothing less from nature.

○ The Basis of Body Temperature Regulation

The body temperature of an organism is a balance between the rate at which heat is supplied and the rate at which it is dissipated. There are two general sources of heat: internal metabolism and the external environment. Losses occur through the skin, the rate of which is influenced strongly by external temperature and insulation (fur, feathers, or fat) and from evaporation associated with respiration (e.g., panting), sweating, and other ways water facilitates transfer of body heat, such as moistening the body with saliva.

○ If Not Warm-Blooded, Then What?

The term warm-blooded was coined to describe the ability of an organism to remain warm, even in a cold environment, by producing heat internally. The term for this is endothermy (Greek endo = inside; therm = heat). Historically, precise control of body temperature was thought to be a characteristic that set man apart from “brutes” (Reeve, 1809), a traditional Judeo-Christian ethic that shaped how we value nature (White, 1967). Mammals or birds that did not maintain a strict temperature were considered inferior; neither nature nor their creator had perfected in them a constant body temperature.

The term warm-blooded is often understood to mean the animal maintains a constant temperature, for which homeothermy (Greek homo = same) is the correct technical term. Homeotherms maintain (defend) a body temperature even in cool or cold environments. They do so mostly by producing heat internally from metabolic conversion of food. Humans are considered an extreme example of a homeothermic endotherm, although there is limited evidence that when exposed to cold, skin and core body temperatures of Australian Aboriginals and Alaculuf Indians drops (Tipton et al., 2008). Humans are good at maintaining a constant body temperature using endogenous (originating from within) heat production, and unfortunately are viewed as the standard against which all other organisms are compared. However, even the benchmark of a constant 98.6°F (37°C) in humans is misleading.

In contrast are “cold-blooded” vertebrates (an equally bad and inaccurate thermal designator): fish, amphibians, and reptiles. The term for this is ectothermy (Greek ecto = outside). Typically, ectotherms are said to have a body temperature that conforms to their environment, and as a group they are often considered to lack the physiological capacity to endogenously generate sufficient heat to maintain a relatively constant body temperature independent of ambient temperature. Nevertheless, ectotherms often maintain a nonconforming body temperate using a variety of behaviors, the best known of which is basking, commonly used by snakes and lizards. However, to add to the confusion, some ectotherms produce heat internally, in other words are endothermic, although they often produce heat only under certain environmental conditions and do not sustain a constant temperature long-term. Bluefin tuna, other deep-sea fishes, some moths, bees, pythons, and probably many dinosaurs were “sometimes endotherms.” So heterotherms (Greek hetero = other or different) are not always ectothermic, and endotherms are not always homeothermic.

Well into the 20th century, it was assumed the human homeothermic endothermy paradigm was widespread among mammals and birds (Scholander et al., 1950). We now know many birds and mammals do not maintain high and constant body temperatures. When an endotherm varies its body temperature to accommodate environmental situations, it is heterothermic—a heterothermic endotherm. In short, mammalian endothermy is not synonymous with homeothermy, and mammals (and birds) use a continuum of (heterothermic) thermoregulatory patterns (Boyles et al., 2013; Levesque et al., 2016).

In summary, yes, it can be a little confusing. “Cold-blooded” animals, better called ectotherms, sometimes produce heat and are endothermic, but they do not maintain a relatively constant body temperature and so are not homeothermic. Similarly, “warm-blooded” animals, better called endotherms, are often considered to maintain a relatively constant body temperature (i.e., are homeothermic), but sometimes have a variable body temperature and thus are heterothermic. But that is our point. Classifying animals as warm- or cold-blooded perpetuates the fundamental misconception that there are two, and only two, thermal answers to a variable environment. There is a continuum of thermal strategies.

○ Mammalian Body Temperatures & Evolution of Endothermy

Therapsids, 300 to 200 million years ago in the Permian and Triassic, gave rise to the mammals, and many inhabited seasonally cold regions of the supercontinent Gondwanaland, where endothermy was essential. Therapsids were stomping around the planet for about 120 million years before dinosaurs ruled in the Jurassic. Therapsids evolved more efficient food absorption, breathing (using a diaphragm), blood circulation (using a four-chamber heart), and energy use (greater aerobic capacity), which allowed better control of internal physiological processes (homeostasis) and greater independence from environmental temperature fluctuations. Late therapsids were similar to modern-day monotremes (platypus and spiny echidna).

Students young and old know that monotremes lay eggs and that marsupials (e.g., kangaroos and opossums) birth tiny undeveloped young; many but not all species have a pouch (or protective folds of skin) where babies develop. And they know that the best, the “real, true, good” mammals have a placenta and carry babies inside their bodies (eutherian mammals). How does this relate to body temperature? Monotremes and marsupials typically have a body temperature that is 1.8–5.4°F (1–3°C) lower and a daily range of body temperatures (3.6–10.8°F; 2–6°C) that is greater than eutherian mammals (0.6–2.4°F; 0.5–1.5°C) (Clarke & Rothery, 2008; Gaughan et al., 2015). To maintain a higher body temperature, the basal (resting) metabolic rate (the amount of energy expended per unit of time) is greater for eutherians than monotremes and marsupials (Dawson et al., 1979). While mammalian body temperature rises during activity and falls during inactivity, the rate of drop is faster for monotremes (Brice, 2009). A stable thermal internal environment arguably is an advantage when growing a fetus.

Mammals are endothermic, but species from most orders use heterothermy. A lot of research on monotremes explores
physiological and ecological adaptations that allow them to be more homeothermic, while an important segment of thermal research on eutherian mammals looks at adaptations that allow them to be more heterothermic. Ironically, the old anthropocentric thermal paradigm classifies the former adaptations as advanced (interpreted as good) and latter adaptations as old (inferior). Is an adaption to an environmental challenge more advanced only if it favors homeothermy? The answer is no. Evolutionarily mammalian heterothermy is sometimes old and sometimes new (Lovegrove, 2012), ecologically heterothermy often better allows survival, and anthropocentrically the question is irrelevant. The energetic cost of remaining homeothermic from endogenous heat production in an environment with a low ambient temperature and limited food may be insurmountable, so the ability to save energy via heterothermy is a great thing to have. But obviously, being a homeothermic endotherm serves some species very well. The value of heterothermia or homothermia depends on the species, the environment, and survival.

How did mammals become endothermic, and why the many differences? Evolution of thermoregulation was like evolution of any trait, such as elongation of horses’ legs allowing them to outrun predators. Advantageous genes survive into future generations, and elements of modern endothermic physiology evolved alongside one another by a series of small incremental shifts (Kemp, 2006). It is hard to understand the benefit of incremental evolution of endothermy without heterothermy (Lovegrove, 2012). For example, a slightly elevated metabolic rate (in an incipient homeotherm) may allow a few more minutes of activity as the environment cools at dusk, but at some point, the slightly elevated metabolic rate is insufficient to maintain homeothermy, and once that happens, the individual is exposed to predation and other environmental risks, if not death from exposure. Dying 7 minutes later does not improve the likelihood that a gene promoting endothermy is passed to the next generation. But a heterothermic strategy would allow a low body temperature in a cold environment to conserve energy and allow rewarming from a combination of exogenous heat, such as basking, and endothermic heat. Heterothermy: a winning evolutionary strategy!

**The Many Faces of Endothermy**

There are two groups of questions about how well endothermy works. Does it keep a whole organism warm over time in a variable environment? Does it keep all parts, like extremities, warm all the time? Readers likely have direct experience with the latter question. If humans are such great homeothermic endotherms, why do they get cold feet?

Even strongly homeothermic species experience varying temperatures on different body parts. During COVID-19, almost everyone went through a portal where they had their forehead temperature taken. If they paid attention, they saw this was usually 0.5–1°F (0.3–0.6°C) lower than the average oral temperature of 98.6°F (37°C) (although this temperature is debated). A body surface that is a bit cooler is a function of temperature exchange at the interface between a warm body and a cool environment, and it saves a bit of energy. Some mammals, like whales, have fat beneath the skin to insulate and further reduce the rate of heat loss. In contrast, after consuming alcohol, blood vessels near the surface dilate, increasing heat loss, and you feel warm and flushed. Rectal and ear temperatures are 0.5–1.0°F (0.3–0.6°C) higher than oral, and axial (armpit) temperature is about the same amount cooler. Our body temperature drops 1–2°F (0.6–1.2°C) at night while we sleep. When we exercise, we get hot, and sweating helps us cool. Which brings us back to the point for taking temperatures. Body temperature often increases when fighting an infection such as COVID, as do areas mending from trauma. Although less well known, body temperature often decreases before increasing when fighting an infection. Even strongly homeothermic species do not maintain a strictly constant temperature over time or across the body.

In addition to fat and fur (or feathers), a variety of anatomical and physiological adaptations help conserve heat and save energy. One well-documented mechanism is countercurrent heat exchange, where heat is exchanged by arteries that are close to veins that flow in the opposite direction. In species where an appendage, like a leg or foot, is exposed to cold, arterial blood going to the foot is cooled by venous blood returning from the foot, so blood arriving at the foot is already cooled, with less heat to lose, conserving energy. So, a homeothermic endotherm has a heterothermic extremity!

There are many times when, and reasons why, a constant body temperature is not advantageous. If it is cool and a species must spend a lot of energy to stay warm, it may be advantageous to allow your body temperature to drop, saving the energy cost of keeping warm. Think of how much you could save on your winter heating bill if you could comfortably turn the heat down to 60°F (15.6°C). There are advantages to being heterothermic even if you are an endotherm, whether it is daily during the coldest part of the night, short cold spells in spring and autumn, or an entire winter.

A cold environment is not the only problem for an organism trying to remain homeothermic. The environment can be too hot. Water is key to solving this dilemma. Water is a thermal sink that facilitates transfer of excess body heat to the environment. Heat radiators come in many forms. Lungs transfer heat to the environment by warming air breathed in and saturating it with moisture that is exhaled. Dogs pant. Some mammals put moisture (sweat, saliva, or urine) on the body surface for evaporative cooling, or they seek out water in the environment, like pigs in mud. Some species have large ears that act as radiators to release heat and help them remain homeothermic. Blood is 50% water, and vessels in the ears are close to the surface and release heat to the environment. Unfortunately, water is rare in some environments, and energy management and conservation is inextricably intertwined with water management and conservation. How do camels survive the heat while using so little water? They use a heterothermic ploy. Their body temperature rises during the heat of the day and cools at night, conserving water, although this physiological tactic is most often used at extremes of food and water deprivation. Desert rodents use heterothermy to save water and energy.

**Torpor & Hibernation**

When endothermic organisms drop their body temperature, go heterothermic, for a few hours or a few days it is typically called torpor. Heterothermy for long periods and at lower temperatures (often winter) is termed hibernation. Characterized by a drastic reduction of the metabolic rate and a decrease in body temperature after passive cooling, torpor and hibernation are unique successes of endothermic heterotherms. They enable animals to survive periods of low resource availability. Torpor and hibernation are used by a diverse group of species of mammals and birds (Clarke et al., 2010; Martin & Yoder, 2014; Geiser, 2020), so it must have value. Mammalian hibernators include monotremes, marsupials,
and eutherians in the orders Carnivora (cats, dogs, weasels, and bears), Rodentia (mice, rats, and squirrels), Afrosoricida (e.g., tenrecs of Madagascar) (Figure 1), Chiroptera (bats), Erinaceomorpha (including hedgehogs), Xenarthra (anteaters, tree sloths, and armadillos), and Primates (lemurs, monkeys, and humans) (McKechnie & Mzilikazi, 2011; Blanco et al., 2013). Birds from at least 13 families are heterothermic, including hummingbirds, nightjars (e.g., whip-poor-wills, common poorwills, and nighthawks), swifts, doves, chickadees, and roadrunners (Figure 2). Birds that rely on a food supply that is unpredictable at cooler temperatures, like insects, nectar, and fruit, are more likely to use torpor.

Hibernation is generally described as an adaptation to seasonally low temperatures when food and/or water are absent or limiting, and is ascribed to species in temperate regions of the world as a cold-winter phenomenon. But that definition is changing as there are tropical hibernators. In addition, during summer in hot dry environments, small mammals use torpor, termed estivation, in cool underground retreats. During hibernation, metabolism is reduced to a fraction of the active homeothermic rate. It allows individuals to survive periods of high energy demand and low energy availability (e.g., winter). Bluntly stated, it slows starvation. Survival is good, certainly better than dying, but it is not without risks and costs, so individuals that store more energy, as fat or food caches, hibernate less.

Hibernation is not without foibles. There is a limit to the value gained from metabolic suppression. Below low temperatures, about 5°C, energy savings are disproportionately small and likely inconsequential (Geiser, 2004), and below this temperature many species raise their metabolic rate to maintain body temperature (Geiser & Broome, 1993; Geiser & Brigham, 2004). Oddly, hibernators must arouse intermittently, and the energy cost of raising the body temperature to a “normal” homeothermic state and maintaining it against a cold environment is disproportionately high compared to heterothermy, and this cost increases as the environment gets colder and body size gets smaller. Thus, arousal is very energy expensive. Some species of bats hibernate in clusters (Figure 3) and sometimes share energetic costs of periodic arousal (Boyles et al., 2008). If arousal is energy expensive, why do it? There are nonenergy costs of hibernation, for example neuronal and chromosomal damage, which are repaired during arousal, so hibernation is a trade-off, balancing benefits of heterothermic energy conservation against other costs.

Small mammals and birds use hibernation and torpor more than large species because smaller animals have a proportionately larger surface area from which to lose heat, despite insulation from fat, and fur or feathers. The rate of temperature change in large animals is slow, limiting the effectiveness of heterothermy. The TV coroner makes this clear by stating the number of hours since death, based on body temperature of an ectothermic corpse. How could a large dinosaur function as a heterotherm if it took many hours to cool?

Homeothermy benefits eutherian reproduction by producing characteristic and dependable timelines for fetal development. Everyone knows human babies are born at 9 months, and farm kids know piglets are born at 3 months, 3 weeks, and 3 days. But torpid mammals have a longer pregnancy (Racey, 1973; Willis et al., 2006). So, isn’t heterothermy contraindicated? Even during reproduction, torpor may allow individuals to survive adverse conditions and limited resources, and so still reproduce. Parturition is delayed until conditions are better for mother and baby. It is a tradeoff, and
evolutionary fitness is served. In some cases, torpor during spring cold spells may help synchronize the phenology of reproduction, which may be valuable, for example when sharing the cost of heating a colonial roost.

In this discussion we considered hibernation and torpor as essentially a continuum of the same phenomenon (Boyles et al., 2013) but some researchers consider them functionally distinct and evolutionarily independent (Ruf & Geiser, 2015; Geiser, 2020). Traditionally, hibernation has been considered predictable, seasonal, and obligatory, with long-lasting torpor bouts and a heavily depressed metabolism, while daily torpor was typically seen as opportunistic, short (few hours), and shallow (metabolism less depressed), often in response to an unpredictable environment. We also focused on mammals at cold temperatures in temperate portions of the world, but many birds are endothermic heterotherms, and species of both mammals and birds use torpor in the tropics. The dwarf lemur, a mammal from Madagascar, and the Puerto Rican tody (a bird) use torpor in tropical environments. While torpor in response to cold temperatures and a limited food supply is somewhat intuitive, why would tropical species use torpor? A variety of environmental conditions can suppress food supplies: seasonally heavy rain or drought, heat, and even cool weather. Further, use of torpor to meet demands of seasonally predictable small, frequent, but still erratic resource constraints is not inherently less valuable than when used for large seasonal events, and arguably, there could be more thermoregulatory phenotypes, even if each is less pronounced.

Parting Hot Thoughts

We hope changing how a small amount of information is provided to young students will broaden life-long understanding of and appreciation for thermoregulation by mammals (and birds). Abandoning the warm-blooded myth sets the stage for understanding the continuum of ways mammals and birds thermoregulate, from homeothermy to heterothermy.

Our goal is aspirational but not unrealistic. As biologists, we say, "Mammals are endotherms; some species are homothermal, and some are heterothermal. Each has advantages and disadvantages for survival." To third-graders we could say, "Mammals make their own body heat. Some species, like humans, stay warm most of the time while the body temperature of other species can sometimes decrease when they do not have enough food to keep warm. One example is when bats hibernate in winter and they have no insects to eat, but there are many others. For some species, staying warm all the time helps them survive, while for other species the ability to change their body temperature helps them survive."

Millions of households put out hummingbird feeders and wonder how those tiny birds made it through a cold snap. Hummingbirds are endotherms that sometimes are heterothermic. Their body temperature drops, and they go into torpor to conserve energy when they do not have enough food energy to maintain a high body temperature in the cold. On a broader scale, why are there so many endemic species of birds in cloud forests of Colombia, which are cold, wet, and inhospitable? Why are so many unique places with species needing protection such hostile environments, and how do species survive in those environments?

Private organizations and public agencies make conservation decisions for local issues, like allowing seasonal construction, and global concerns, like climate change. How are mammals and birds that use torpor to survive difficult times impacted by these decisions? A better understanding of thermoregulation may inform decisions by conservation organizations and regulatory agencies when protecting and managing unique ecological habitats, particularly thermally unique habitats. Decision-makers do not need to be experts, but they do need basic knowledge to ask questions and know when, perhaps, to seek involvement of an expert.

Everyday wonders of thermoregulation abound: dogs pant, humans sweat, pigs lay in mud, camels survive desert heat, ducks have cold feet, jack rabbits have big ears, and the axillary temperature of a child who refuses an oral thermometer is different than oral temperature. Did human ancestors hibernate? Can we hibernate to go into space? What might we learn from daily or intermittent torpor about intermittent fasting, a frequent part of a ketogenic diet? Do you burn more calories and lose weight in fall than used for large seasonal events, and arguably, there could be more thermoregulatory phenotypes, even if each is less pronounced.

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