

# THERMOREGULATION, ENERGETICS, AND BEHAVIOR

*Christopher Harshaw, Mark S. Blumberg, and Jeffrey R. Alberts*

Temperature affects all aspects of biological function, including behavior (see Haynie, 2001). All behavior thus occurs within a thermodynamic context and is bounded by thermal and energetic constraints (see Careau, Killen, & Metcalfe, 2015; Mathot & Dingemans, 2015). Some of these arise within biological systems, directly out of the mechanics of physics, biochemistry, and geometry. For example, chemical reaction rates are temperature dependent, as are many critical characteristics of enzymes and other proteins, including structure and function. The same is true for many properties of biological membranes (Hazel, 1995), including the permeability of chorionic and amniotic membranes (e.g., Bara & Guiet-Bara, 1986) and the blood–brain barrier (Kiyatkin & Sharma, 2009). There are thus thermal optima for the myriad functions and complex biochemical reactions that drive living systems—optima that are carefully balanced and adjusted dynamically in the face of internal and external challenges.<sup>1</sup>

Neurons are among the most temperature-sensitive cells in the body (Kiyatkin, 2010; Rango, Arighi, & Bresolin, 2012). Many critical parameters of neuronal functioning (e.g., conduction velocity, refractory period) covary with temperature, implying coupling between brain temperature and neural processing (e.g., Blessing, Mohammed, & Ootsuka, 2012, 2013; Thiessen, 1983a) and optima for neuronal functioning (see Gisolfi & Mora, 2000; Kiyatkin, 2010). Indeed, the energetic efficiency of action

potentials improves with increased temperature within the mammalian physiological range, with optimal efficiency at 37° C (Yu, Hill, & McCormick, 2012). Even small elevations (3° C–4° C) above this (e.g., because of fever, stroke, or ingestion of drugs such as MDMA [3,4-methylenedioxymethamphetamine]) can trigger neuronal dysfunction resulting in hallucinations, seizures, and damage (e.g., Brown & Kiyatkin, 2004). Likely because of these trade-offs, some of the most fascinating thermoregulatory adaptations have emerged in the context of regulating brain temperature (see Blumberg, 2002).

Other constraints on temperature regulation are imposed from outside the animal. For example, by beginning life in the same locale in which their parents reproduced, most animals inherit basic ecological and climatic conditions and, within that context, select among or create microclimates. Add to this variation from daily and seasonal temperature rhythms, and we can recognize the bases of complex and varied adaptive strategies. In response to seasonal changes, some species migrate; others hibernate, estivate, or become hypometabolic (see Storey, 2015); many show season-specific changes in fur density, fat composition, and other metabolic and thermoregulatory phenotypes (Blumberg, 2002). With respect to daily changes, most species exhibit closely coordinated circadian rhythms of behavior and physiology, thereby optimizing the acquisition, utilization, and conservation (or loss) of thermal energy. For example, on a

<sup>1</sup>For example, pathogens frequently elicit *fever* (an adaptive elevation of body temperature; Kluger, Kozak, Conn, Leon, & Soszynski, 1998), whereas hypoxia and exposure to toxins generally trigger *anapyrexia* (an adaptive lowering of body temperature; see Branco, Gargaglioni, & Barros, 2006; Gordon & Rowsey, 2009).

hot summer day a chacma baboon (*Papio ursinus*) may opt to lounge in the cooler microclimate provided by shade, adjusting its “activity budget” to minimize heat gain and simultaneously maximize compatible behaviors such as grooming and resting (Hill, 2006).

Another example of an exogenous thermoregulatory constraint is the thermal inadequacy of conditions under which laboratory mice (*Mus musculus*) are often housed and studied: The ambient temperatures commonly maintained in laboratories and rodent vivaria (typically 20° C–22° C), although comfortable to humans, present a significant cold challenge to mice and other small rodents. The result is metabolic stress, particularly when animals are housed alone or with inadequate nesting material (e.g., Gaskill et al., 2012; Gordon, 2004). In several classic yet largely forgotten studies, individually housed mice showed decreased growth as well as increased incidence of skin disease and tumors compared with mice housed in groups (e.g., Andervont, 1944; Retzlaff, 1939). Such effects were attributed in part to the thermal and metabolic consequences of group housing (cf. Prychodko, 1958)—an interpretation supported by recent studies indicating that mice show multiple impairments in immune regulation and cancer defense under typical housing conditions because of cold-stress (Eng et al., 2015; Kokolus et al., 2013, 2014). Clearly, there is reason for concern that ambient temperature can alter outcomes not only in preclinical cancer studies but also in biomedical and behavioral research more generally (see Maloney, Fuller, Mitchell, Gordon, & Overton, 2014; Messmer, Kokolus, Eng, Abrams, & Repasky, 2014). Indeed, the previously mentioned danger of MDMA for brain temperature and neuronal survival is similarly modulated by social and ambient thermal context (see Kiyatkin, 2014).

That temperature is such a pervasive moderator of animal behavior and physiology is unlikely to surprise comparative psychologists, who traditionally attend to details of natural history, ecology, and development (e.g., Beach, 1950; Schneirla, 1966). Nevertheless, most “translational” research (i.e., focused on relevance to human health; see Gottlieb & Lickliter, 2004) is conducted largely

without the perspective of comparative psychology. Many investigators view organisms, biological mechanisms, and behaviors as dissociable from biological context (the ecologies and niches in which animals develop and evolve). As highlighted previously, this can lead investigators to overlook critical variables, such as *ambient temperature*, when considering issues of animal husbandry and experimental design, and when interpreting results (cf. Timberlake, 2004). For example, Blumberg (2001) noted that psychobiologists working within different domains (e.g., sleep, learning and memory) have often settled on testing infant subjects at air temperatures that provide the best context for eliciting the particular behavior of interest—a case of “reverse-reinforcement” in which the subjects train the experimenters. Nevertheless, when such tweaks of design are ignored when data are interpreted, an inaccurate or skewed appreciation of organismal capabilities can result (Blumberg, 2001; Satinoff, 1991; Timberlake, 2004).

In the remainder of this chapter, we provide further evidence regarding the fundamental importance of ambient thermal conditions and thermoregulation for comparative psychology, behavioral neuroscience, and related fields. In particular, we advocate for paying close attention to context, including species-specific and developmental differences in thermoregulatory niches and adaptations. We review the topic of thermoregulation by first covering basic concepts and terminology important for a comparative understanding of thermoregulatory adaptations. In successive sections, we situate thermoregulation within ecological context, chronobiological and circadian context, and developmental and social context. These are not separate levels of analysis, but rather overlapping and interrelated contexts within which thermoregulatory physiology and behavior must be understood.

## THERMOREGULATION: BASIC CONCEPTS

Individuals in most of the popular model species prefer and, if provided a choice, seek a relatively restricted range of thermal conditions.<sup>2</sup> Zebrafish (*Danio rerio*), for example, prefer ambient temperatures of 24° C–30° C (Lawrence, 2007).

<sup>2</sup>There are a variety of ways to measure temperature preference, most of which have been applied to only a handful of species that can be tractably studied under laboratory conditions.

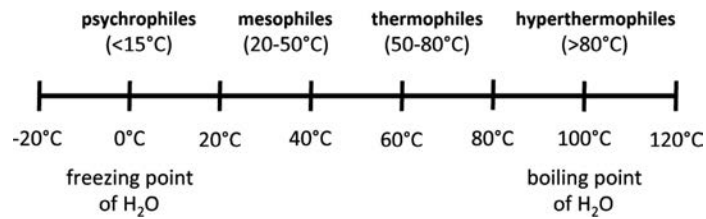


FIGURE 45.1. A depiction of the range of temperature preferences found in nature, along with terminology that is generally applied primarily to taxa that are distributed widely throughout this range (e.g., bacteria, algae, fungi; see Wintrobe & Arnold, 2000). Above 60° C these are exclusively prokaryotic (Tattersall et al., 2012).

Adult house mice (*Mus musculus*) and rats (*Rattus norvegicus*) prefer temperatures of 26° C–29° C and 24° C–30° C, respectively (see Gaskill, Rohr, Pajor, Lucas, & Garner, 2009; Gordon, 1994).<sup>3</sup> A survey of all known organisms would nonetheless reveal an impressively large array of preferences (see Figure 45.1), with niches ranging from 20° C to 120° C. Moreover, an even broader range of temperatures can be tolerated by various species. The upper and lower bounds for such tolerance—beyond which homeostatic regulation fails—are termed the *critical temperature minimum* and *critical temperature maximum* (see Terblanche et al., 2007). As can be seen in Figure 45.1, species that prefer moderately warm temperatures, inclusive of the ranges previously mentioned, are termed *mesophiles*. Organisms that prefer the hottest (>80° C) and coldest (<15° C) temperatures (so-called *extremophiles*) are termed *hyperthermophiles* and *psychrophiles*, respectively (see Wintrobe & Arnold, 2001).

Diverse strategies are used to optimize physiology, survival, and reproduction under such varied thermal conditions (see Tattersall et al., 2012). The most general are *ectothermy* and *endothermy*. Ectotherms are organisms that do not produce substantial amounts of heat internally and thus rely on external sources of heat to meet their thermal requirements. Endotherms, on the other hand, possess endogenous means for producing heat (e.g., shivering and nonshivering thermogenesis). For endotherms, temperature preferences are often tied to what is referred to as the *thermoneutral zone*, or

the range of ambient temperatures in which energy expenditure for metabolic heat production (*thermogenesis*) and heat retention (*thermolysis*) are at a minimum (Satinoff, 1996). At *thermoneutral air temperatures*, body temperatures are thus stabilized, usually above ambient temperatures, and maintained via energetically inexpensive adjustments (e.g., vasoconstriction, vasodilation; Kingma, Frijns, Schellen, & van Marken Lichtenbelt, 2014).

Importantly, behavior makes critical contributions to thermoregulation. This includes *thermotaxic* responses (i.e., moving toward or away from heat; Fraenkel & Gunn, 1942) and postural adjustments (e.g., sprawling, curling up), as well as aggregative behaviors such as huddling. In this context, ectotherms are sometimes depicted as passive thermoregulators and endotherms as active thermoregulators (e.g., Balter, 2014). In fact, both are equally active in using behavior to regulate body temperature (cf. Bogert, 1949; Satinoff, 1996). For example, reptiles are ectotherms and have long been caricatured as “cold-blooded,” yet they use behaviors such as positive thermotaxis (moving toward warmth), basking (*heliothermy*), burrowing, and aggregating with others of the same species to regulate their body temperatures within narrow limits (e.g., Bogert, 1949; Burghardt, 1988; Dee Boersma, 1982) and to produce fevers in response to infection (see Kluger, 1979). Humans, on the other hand, are endotherms and yet rely on a diverse external means—including clothing, housing, air conditioning, and drinking of cool and

<sup>3</sup>Importantly, there are also a number of factors, including circadian cycle, body size, and sex, that also significantly influence such preferences (e.g., Gaskill, Rohr, Pajor, Lucas, & Garner, 2011; Gordon, Becker, & Ali, 1998).

warm liquids—to maintain thermal equilibrium and comfort.

Another common distinction is between *heterothermy* and *homeothermy* (see Tattersall et al., 2012). Homeotherms are organisms that regulate body temperature within relatively narrow bounds, in defense of what is frequently thought of as a single core body temperature ( $T_b$ ). The word *relatively* is important here, given that all homeotherms show significant circadian and, frequently, ultradian (shorter than 24 hr) cycles in body and brain temperature (e.g., Blessing et al., 2013; McFarland et al., 2015). Additionally, there are numerous local and independently regulated body temperatures (e.g., brain, abdominal, muscle, scrotal) that render the notion of a single defended  $T_b$  misleading (see Blumberg, 2001). Heterotherms, in contrast, display more labile body temperatures and regulate  $T_b$  at more than one level. For example, a heterotherm may regulate  $T_b$  at a high level during the part of the day or year when it can obtain the most energy from its environment (and often reproduce most successfully) but go into torpor or hibernation—significantly lowering  $T_b$ , oxygen consumption and energetic requirements—for the rest of the day or year, respectively.<sup>4</sup> The degree to which a particular species or sex (e.g., Cryan & Wolf, 2003) exhibits heterothermy depends on many factors, including body size, the availability of energetic and water resources, and whether or not members of the species hoard food (see Boyles et al., 2013; Hetem, Maloney, Fuller, & Mitchell, 2016). Many mammals thus exhibit greater heterothermy in winter than spring (e.g., Hetem et al., 2016; McFarland et al., 2015)—a pattern that can be reversed in more equatorial species (Boyles et al., 2013).

Among the most basic factors affecting thermoregulation are body size, shape, and surface-to-volume ratio (Blumberg, 2002; Porter & Kearney, 2009). The *surface law* describes the inherent geometrical relation between the volume of an object and its surface area: As body size (or volume) increases, the relative surface area of that object

decreases. This fundamental law governs numerous biological processes, including gas exchange in the lungs and photosynthesis in the leaves of trees, limits on the size of single cells, and the loss (and gain) of heat from animals of different sizes (Gould, 1966; Thompson, 2014). It explains why dead elephants take days to cool to room temperature and dead mice only hours. By extension, the law also sets constraints on the relationship between body size and basal metabolic rate (see Schmidt-Nielsen, 1984) as well as the relationship between body size and various aspects of life history, such as reproductive output (see Speakman & Król, 2010). The high *thermal inertia* of large animals such as elephants (*Elephantidae*) and leatherback turtles (*Dermochelys coriacea*) places them in a distinct thermoregulatory niche; indeed, a large ectotherm like *Tyrannosaurus rex* could have approximated homeothermy because of its ability to retain heat (Gould, 1966; Sato, 2014). This fact has given rise to the term *gigantothermy* to describe the regulatory strategy of such giants (see Paladino, O'Connor, & Spotila, 1990).

The fine details of morphology also bring thermoregulatory consequences and trade-offs (Davenport, 1992; Porter & Kearney, 2009). For example, the enlarged ears of elephants and many desert animals, such as the fennec fox (*Vulpes zerda*), have utility for hearing and heat dissipation (e.g., Phillips & Heath, 2001). The conspicuous horns, frills, and antlers of organisms as diverse as bovines, deer (*Cervidae*), and dung beetles (*Onthophagus binodis*)—features usually thought of primarily as weaponry—similarly have an important influence on heat exchange and thus brain and body temperatures (e.g., Shepherd, Prange, & Moczek, 2008). Another example can be seen in the tails of rodents, such as rats and mice; because of the tail's lack of fur and large surface-to-volume ratio, it provides an extremely efficient means of dissipating heat, particularly when combined with mechanisms for selective vasoconstriction and vasodilation (e.g., Dawson & Keber, 1979).<sup>5</sup> The

<sup>4</sup>An additional term, *mesothermy*, has been introduced by Grady et al. (2014) to describe an intermediate strategy, involving the raising of  $T_b$  via internal metabolism and lack of defense of a particular set point. This strategy appears to have been adopted by dinosaurs and a few extant animals, including sharks and leatherback turtles (see Grady et al., 2014).

<sup>5</sup>Without tails, rats and mice show significantly reduced heat tolerance and higher incidence of death if challenged with heat (e.g., Stricker & Hainsworth, 1971)

flattened tails of beavers (genus *Castor*) similarly serve as a critical radiator of excess heat (Steen & Steen, 1965).

Body composition is also critical for thermoregulation. Integumental features such as layers of fat and blubber serve as insulators, slowing the rate of convective heat exchange with the environment. Muscular activity also contributes to thermoregulation by generating heat through normal use; in addition, muscles are recruited specifically for heat production during shivering in mammals (Hemingway, 1963) as well as preflight and presinging warm-up in insects (e.g., Heinrich, 1993). *Uncoupling proteins* (UCPs) are an important and widespread molecular innovation that permits the uncoupling of mitochondrial respiration from ATP synthesis, allowing proton leakage and the release of energy as heat (see Argypoulos & Harper, 2002). UCPs make critical contributions to *thermogenesis* in animals as diverse as bats (*Chiroptera*), cetaceans, humans, and even some plants. For example, the skunk cabbage (*Symplocarpus foetidus*) uses UCPs to keep its reproductively vital spadix warm during the cool conditions of early spring (Ito, 1999), whereas cetaceans and birds use UCPs in their blubber and skeletal muscle, respectively (e.g., Hashimoto et al., 2015).

Brown adipose tissue (BAT) is a particularly interesting modification of muscle tissue (i.e., it stems from muscle rather than adipocyte progenitors) that uses lipid stores and abundant mitochondria, in conjunction with a particular uncoupling protein (i.e., UCP1), to produce large quantities of heat (Cannon & Nedergaard, 2004). BAT was originally discovered in bats and other hibernators and thus was long considered a hibernating gland. For example, during hibernation, ground squirrels (*Ictidomys tridecemlineatus*) rely on UCP1 in BAT and in their neurons, allowing these squirrels to keep their brains warmed to a temperature well above their  $T_b$  (Laursen et al., 2015). Nevertheless, BAT is now known to have functions that extend far beyond hibernation, making important contributions to thermoregulation, energy expenditure, and weight regulation under a wide range of conditions

(see Cannon & Nedergaard, 2010). The swordfish (*Xiphias gladius*), a large pelagic predator that routinely experiences wide fluctuations in water temperature, for example, uses a tissue similar to BAT at the base of its brain to direct heat to its brain and eyes so as to maintain visual acuity (Carey, 1982).

Surface features such as pigment, feather, fur, and hair can have similarly important consequences for convective and radiative heat transfer (see Davenport, 1992). For example, in the cold, the fluffing of feathers in birds and fur in mammals traps and immobilizes air and thus significantly improves insulation.<sup>6</sup> Even the sparse hairs on elephant skin influence convective heat transfer (Myhrvold, Stone, & Bou-Zeid, 2012), much the same as spines do for cacti in desert environments (Nobel, 1978). The wrinkles and crevices in elephant skin similarly serve not only to increase the total surface area available for heat exchange but also to trap and channel water, thereby improving evaporative heat loss (Lillywhite & Stein, 1987). By comparison, the relatively smooth skin of dolphins and other small *cetaceans* minimizes not only drag but also the transfer of heat (Boily, 1995).

Glandular secretions likewise significantly affect thermoregulation. In species with sweat glands living in hot, dry conditions, fluid excreted as sweat evaporatively cools the body (see Houser, Crocker, & Costa, 2005). Salivary and nasal glands make similar contributions across a wide variety of species. For example, in dogs (*Canis familiaris*) and many other nonsweating species, nasal glands secrete fluid during panting, improving the efficiency of evaporative cooling (see Richards, 1970). Similarly, in species including rats, mice, and other rodents, saliva is secreted copiously under warm conditions and actively groomed into the fur, facilitating cooling (e.g., Stricker & Hainsworth, 1971). In tortoises (*Testudinidae*) and other turtles, salivation and urination are used to similar effect (e.g., Riedesel, Cloudsley-Thompson, & Cloudsley-Thompson, 1971).<sup>7</sup> In contrast, Mongolian gerbils (*Meriones unguiculatus*) secrete lipids and pigment from the Harderian glands under cool conditions,

<sup>6</sup>This behavior also occurs in other contexts (e.g., to produce fever in response to infection).

<sup>7</sup>Many species of monkey have also been observed to use urination and “urine washing” to apparently aid evaporative cooling (e.g., Roeder & Anderson, 1991).

which are mixed with saliva and groomed into the fur, facilitating the absorption of radiant heat from the sun (see Pendergrass & Thiessen, 1981).

Clearly, animals have evolved diverse means for regulating metabolic and thermal exchange with their environments.<sup>8</sup> Despite the likely strong selection for such traits, *plasticity* in thermoregulatory phenotypes over smaller timescales is common, as it occurs in season-of-birth effects (involving *epigenetic programming*), acclimatization, and cold adaptation (see Clarke, 1991; Seebacher, 2005; Tattersall et al., 2012). When bred and reared under cold conditions (e.g., 0° C –5° C), for example, rats and mice show distinct adaptation to cold, including larger body size, shortened tails, and increased thermogenic capacity of BAT (e.g., Nedergaard, Alexson, & Cannon, 1980). Importantly, such experience-dependent plasticity can produce variation within a given species that is more pronounced than average differences observed between species (Seebacher, 2005; see also Chapters 11 and 18, this volume).

Given their potential to trigger adaptive plasticity, laboratory thermal conditions can thus interfere with or even mask the effects of experimental manipulations, including those involving the inactivation or “knockout” of genes (see Feldmann, Golozoubova, Cannon, & Nedergaard, 2009; Gordon, 2004). For example, when mice with the UCPI gene inactivated (UCPI<sup>-/-</sup>) were first produced, it was expected that they would be unable to maintain body temperature when cold challenged and that they would also be prone to obesity, because of a loss of energy expenditure via BAT thermogenesis (Feldmann et al., 2009). Compared to wild-types, UCPI<sup>-/-</sup> mice did indeed have difficulty when faced with an acute 4° C cold exposure. However, they did not show the expected obesity phenotype (Enerbäck et al., 1997). Moreover, they were fully capable of adapting to cold if temperature was lowered gradually to 4° C (e.g., Golozoubova et al., 2001); this feat was accomplished by the emergence of a supernormal, marathon shivering ability in these animals (Golozoubova et al., 2001), albeit at the cost of elevated

oxygen consumption and greater oxidative stress (e.g., Stier et al., 2014). Moreover, when UCPI<sup>-/-</sup> mice were reared at temperatures significantly warmer than standard laboratory conditions they became obese, as had originally been predicted (Feldmann et al., 2009). As this example highlights, thermoregulatory behavior and physiology can only be accurately evaluated in relation to specific thermal and energetic contexts. Importantly, these contexts vary over time (e.g., circadian, seasonal, developmental) as well as with the ecological and social features of an organism’s niche.

### THERMOREGULATION IN ECOLOGICAL CONTEXT

Different environments present distinct challenges to thermal homeostasis (see Seebacher, 2005). Newton’s law of cooling states that the rate of heat transfer between a body and its environment will be proportional to the *thermal gradient* between the two. In natural systems, the steepness of such gradients depends on the nature and speed (bulk motion or *advection*) of the surrounding medium, usually air or water. Different mediums conduct heat more or less rapidly (e.g., water conducts heat 25x more effectively than air; Tattersall et al., 2012). At the same time, different levels of bulk motion (e.g., current, wind) influence the thickness of the boundary layer that will separate the animal from ambient thermal conditions. Under conditions of rest and limited airflow, animals on land thus live in and experience a *microclimate* constituted by the thermal boundary layer—influenced by conduction, evaporative cooling, and so forth—rather than “true” ambient conditions. However, wind or quick motion (e.g., running, riding a bicycle) can rapidly strip away this layer, producing a steeper gradient and more rapid heat transfer (e.g., wind chill; Hill, 2006).<sup>9</sup> Conversely, humidity can have a dramatic negative impact on the efficiency of evaporative cooling in hot environments, interfering with the formation of a salutary thermal boundary layer.

<sup>8</sup>It is important to note that there are a number of other important thermoregulatory mechanisms and adaptations, including countercurrent heat exchange and retes (see Blumberg, 2002).

<sup>9</sup>The combination of conduction and advection constitutes *convection*.

Within these global constraints, physical resources such as water, sand, soil, rocks, trees, and other plants can become valuable thermoregulatory resources (e.g., as shelters, or *thermal refugia*, nesting material). The spatial and temporal distribution or *patchiness* of such resources can thus place significant constraints on thermoregulation. Postural adjustments are often used in conjunction with trees, other objects, and even conspecifics to regulate exposure to wind (e.g., Stelzner & Hausfater, 1986). Such objects also provide valuable shade under hot conditions and can, additionally, function as critical heat sinks—being warmer or cooler than ambient conditions, depending on season, surface-to-volume ratio, and other factors. For example, under hot conditions, koalas (*Phascolarctos cinereus*) more frequently hug the cool trunks of large trees, thereby improving heat loss (Briscoe et al., 2014). In addition to being used for creating burrows and hibernacula, sand and soil are often used for bathing. That is, just as bathing in water has thermal benefits in a hot environment (e.g., increasing evaporative cooling) bathing in dust or sand can also bring thermal benefits, particularly if the bathing substrate is cooler than ambient air. For example, by sandbathing on hot days, hamadryas baboons (*Papio hamadryas*) are able to temporarily thwart a rise in body temperature (Brain & Mitchell, 1999).

For these reasons, the ecosystem and physical landscape (including latitude, altitude, and climate) can dramatically influence thermoregulation. Species living in open habitats (e.g., desert, savanna) must cope not only with high temperatures during the day and higher radiant heat loads, but with large diurnal variation (i.e., far cooler temperatures at night) and a limited supply of thermal refugia and heat sinks, apart from those provided by burrows, sand, soil, and so on. For example, the desert grasshopper (*Taeniopoda eques*) relies on a combination of postural adjustments (strategically aligning its body relative to the sun) and microclimate selection to achieve thermal homeostasis (Whitman, 1988). Species in tropical forest environments, on the other hand, must cope not only with high temperatures but also high humidity and reduced bulk motion of air and thus reduced opportunity for convective and evaporative cooling.

## THERMOREGULATION IN CIRCADIAN CONTEXT

The evolution of endothermy in mammals and birds carried with it enormous increases in energetic costs and a corresponding need to manage those costs as efficiently as possible. Indeed, citing a need to offset the energetic demands of waking, one of the more popular and persistent theories of sleep—whose complex manifestations are most evident in endothermic mammals and birds—is that it is a state of energy conservation (Berger & Phillips, 1993; see also Chapter 29, this volume). The rationale for this theory rests on the intuitive notion that sleep, as a period of rest and relaxation, appears to entail decreased energy use. But appearances can be deceiving and they certainly are in this case. In fact, sleep provides only modest energy savings in relation to wakefulness. Moreover, during rapid eye movement (REM) sleep, energy use by the brain is at wake-like levels.

Sleep, especially REM sleep, has a complex relation to the thermoregulatory system (Heller, 2005). For example, during REM sleep, thermoregulatory effectors such as panting, shivering, and sweating are profoundly inhibited, rendering the animal functionally but temporarily ectothermic (Parmeggiani, 2003). It is this feature of REM sleep that likely makes it so sensitive to air temperature: When temperatures are too hot or too cold, transitioning from non-REM to REM sleep is prevented. Moreover, even within a range of thermoneutral temperatures where oxygen consumption is stable, adult rats double their REM sleep time over the air temperature range of 25° C–31° C (Szymusiak & Satinoff, 1981). The extreme sensitivity of sleep to changes in temperature is perhaps most apparent in small infant mammals whose thermoregulatory capacities are limited compared to those of adults (Blumberg & Stolba, 1996; Sokoloff & Blumberg, 1998); maintaining adequate warmth is critical for the neonatal expression of myoclonic twitching during REM sleep, a behavior that is well suited to contribute to the development and refinement of the sensorimotor system (Blumberg, 2015; Tiriach, Del Rio-Bermudez, & Blumberg, 2014).

Adopting a broad view of the energetics of daily activity cycles, Schmidt (2014) introduced his energy allocation theory of sleep. At the heart of this theory is the notion that various biological processes are best performed during sleep or wake and that animals—on the basis of life-history variables such as body size, metabolic rate, reproductive biology, and ecology—have evolved to maximize energy efficiency. Animals thus resolve the inherent energetic trade-offs by adopting one of three general modes of life: sleep–wake cycling, torpor or hibernation, and prolonged wakefulness (Schmidt, 2014). For animals that cycle between sleep and wake, Schmidt has bypassed the traditional view of sleep as a period of energy conservation, with its associated inadequacies. Instead, he argues, animals that adopt this mode of life use periods of sleep to perform various functions (e.g., cellular repair, memory consolidation) that are not ideally performed during wakefulness (Schmidt, 2014). This perspective fits nicely with gene expression studies showing that particular subsets of genes are differentially expressed during sleep and wake (Cirelli, Gutierrez, & Tononi, 2004). For example, genes up-regulated during wake include those associated with metabolism and cellular stress, whereas those up-regulated during sleep include those associated with brain protein synthesis, myelin formation, and synaptic vesicle turnover (Cirelli et al., 2004).

In contrast with sleep–wake cyclers, some mammals and birds adopt the strategy of daily torpor, in which body temperature is allowed to decrease considerably at the same time each day (Geiser, 2004). In relation to torpor, hibernation entails larger decreases in body temperature and longer periods of time. Both approaches are nevertheless similar in that they produce substantial energy savings, albeit with costs. Finally, Schmidt considers the mode of prolonged wakefulness to be the most extreme in terms of its energetic burden, but some animals cannot avoid it if they are to accomplish critical tasks. For example, migratory songbirds exhibit prolonged periods of wakefulness during their long flights (Rattenborg et al., 2004).

## THERMOREGULATION IN SOCIAL CONTEXT

Except under very specific laboratory conditions (i.e., germ-free), animals never occur in isolation. Individual physiology and behavior is thus best understood within the context of an organism's overall *social ecology*, which includes all other organisms with which it interacts—including microbial and parasitic “old friends” (e.g., Rook, Lowry, & Raison, 2013). Brischoux et al. (2009) recently introduced the term *kleptothermy* to describe the thermoregulatory strategy use by organisms that steal heat produced by others. The sea krait (*Laticauda laticaudata*), for example, obtains heat by slithering into the nests of sea birds and can thus be seen as a kind of metabolic parasite (Brischoux et al., 2009). Although kleptothermy arguably adds an unnecessary tinge of moralizing to the description of such relationships, the term highlights the intricate metabolic and thermal entanglement of organisms as they occur in natural contexts.

There are, in fact, myriad symbiotic relationships of varying degrees of mutuality that involve metabolic and thermal exchange. For example, mitochondria, the energetic powerhouses of eukaryote cells, entered into the eukaryotic lineage as endosymbionts. Commensal gut microbiota similarly make contributions not just to host metabolism but also aspects of thermal homeostasis in many animals (e.g., Harrison & Hewitt, 1978; Kluger, Conn, Franklin, Freter, & Abrams, 1990). Megapodes such as the Australian brush-turkey (*Alectura lathami*) externalize a similar relationship when they gather leaf litter into large mounds and make use of the heat generated by microbial decomposers therein to incubate their eggs (Seymour & Bradford, 1992). Likewise, the young of many species exist in a state of obligatory metabolic and thermal symbiosis with parents (e.g., J. R. Alberts & Gubernick, 1983), a situation that can undoubtedly lead to parent–offspring conflict (e.g., Schino & Troisi, 1998) but can also, in theory, have short-term advantages for parents. For example, by ingesting pup urine and feces, rat dams reclaim vital nutrients that would otherwise be wasted, reducing the need for dams to leave the protection of the nest and burrow to forage (J. R. Alberts & Gubernick, 1983).



The social lives of animals are thus inextricably linked with their metabolic and thermoregulatory lives (e.g., Allee, 1938). For example, there is a close coupling between ambient temperature and the allocation of time to social behavior in nonhuman primates (e.g., Hill, 2006; Majolo, McFarland, Young, & Qarro, 2013). Similarly, there is a close coupling between temperature and both activity levels and agonistic interactions (i.e., aggression) in many species (e.g., Greenberg, 1972). For example, a study of giant danios (*Danio aequipinnatus*), a tropical fish, found that changes in water temperature significantly impacted both overall activity levels and aspects of shoaling behavior related to sociality, such as spatial proximity of fish in the shoal (Bartolini, Butail, & Porfiri, 2015).

W. C. Allee (1931, 1938) was among the first behavioral biologists to include the social environment in his analysis of individual physiology and behavior. One of the key insights achieved by Allee and colleagues (e.g., Allee, 1934; Retzlaff, 1939; Nicolás, Martínez-Gómez, Hudson, Bautista, 2011) was that animals—whether bees, fish, rats, or mice—often fair better in terms of health and fitness when they live in stable and moderately sized social groups compared to small and unstable groups or conditions of social isolation. Although there are many benefits of social proximity (e.g., improved predator detection, increased foraging efficiency), among the most important are reduced homeostatic stress because of reduced exposure to ambient conditions and creation of more favorable microclimates. Numerous examples of such advantages are known, including the improved *energetic efficiency* of fish when swimming in schools and human cyclists when riding in dense packs (e.g., Marras et al., 2015). Similarly, a group of huddling individuals functions metabolically as if it were a single larger organism, with increased mass and relatively reduced surface area (Pearson, 1947)—a situation that results in a reduction in water loss under dry conditions (e.g., Boratyński, Willis, Jefimow, & Wojciechowski, 2015) and heat loss and energy use under cool conditions (e.g., Canals, Rosenmann, & Bozinovic, 1989; Harshaw & Alberts,

2012). Huddling groups also produce a significantly warmer microclimate—particularly in the center of the group—further reducing exposure to cold (see Satinoff, 1996).

For these reasons, *social thermoregulation* via huddling, crowding, and clumping is found in numerous species, including many insects, birds, and rodents (see Gilbert et al., 2010). Huddling also appears to be common in nonhuman primates, particularly at night and during the winter (see Anderson, 1984). For example, cold-induced huddling has been documented in baboons (e.g., *Papio papio*), lemurs (e.g., *Eulemur fulvus rufus*), galagos (e.g., *Galago moholi*), and many monkeys (e.g., *Macaca fuscata*, *Rhinopithecus bieti*; e.g., Li, Ren, Grueter, Li, & Li, 2010). Moreover, access to huddling partners appears to be influenced, in many cases, by an individual's social rank or level of integration within the group (e.g., McFarland et al., 2015; Takahashi, 1997). For example, female vervet monkeys (*Chlorocebus pygerythrus*) that had more social partners experienced less hypothermia and a reduced 24 h amplitude in core body temperature (i.e., better homeothermy) during cold winter months than females with fewer social partners (McFarland et al., 2015; see also Chapter 43, this volume)—benefits almost certainly mediated by nighttime huddling (see McFarland & Majolo, 2013). Honeybees (e.g., *Apis cerana japonica*) similarly rely on social thermoregulation via crowding to survive cold winter conditions (Heinrich, 1981; Stabentheiner, Pressl, Papst, Hrassnigg, & Crailsheim, 2003).<sup>10</sup>

Temperature can also place significant constraints on social signaling and communication (see Ophir, Schrader, & Gillooly, 2010; Thiessen, 1983a). Chemical, electrical, and acoustic signals travel more rapidly and cover greater distances under warmer ambient conditions (e.g., A. C. Alberts, 1992). In the case of chemical communication (see Volume 2, Chapter 4, this handbook), temperature also impacts a number of important parameters of chemosensory signals, including quantity released, vapor pressure, and half-life. Honeybees (*Apis mellifera carnica*) appear to harness such relationships in service of nestmate

<sup>10</sup>The Japanese honeybee (*Apis cerana japonica*) displays a weaponized form of crowding whereby bees mob and form a ball around invading giant hornets (*Vespa mandarinia*), generating lethal temperatures (e.g., 47° C; Ono, Igarashi, Ohno, & Sasaki, 1995).

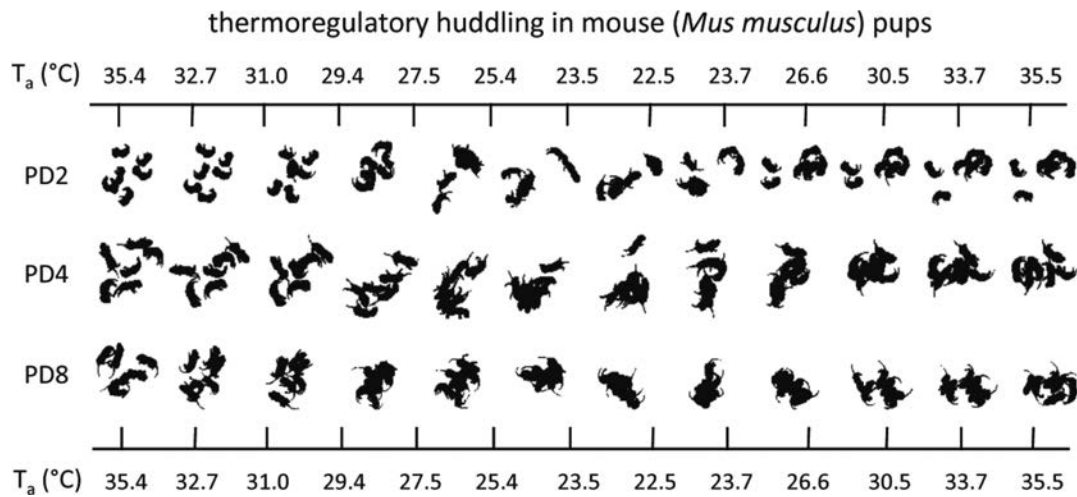


FIGURE 45.2. An example of behavioral thermoregulation via huddling in postnatal day 2, 4, and 8 mouse pups during a temperature cycle from 35.5° C to 22.5° C and back to 35.5° C. As can be seen, there is a clear progression in which pups rapidly attain sophisticated and mature coupling of their huddling behavior to changes in ambient air temperature over the course of the first postnatal week. From “Group and Individual Regulation of Physiology and Behavior: A Behavioral, Thermographic, and Acoustic Study of Mouse Development” by C. Harshaw and J. R. Alberts, 2012, *Physiology and Behavior*, 106, p. 673. Copyright 2012 by Elsevier. Adapted with permission.

recognition: Bees entering the hive display intense thoracic heating (up to 2°C) while being inspected by hive guards, whereas guards cool their thoraxes while performing inspections of arriving bees (e.g., Stabentheiner, Kovac, & Schmaranzer, 2002).<sup>11</sup>

Importantly, temperature also affects the energetic costs of signaling (see Gillooly & Ophir, 2010; Prestwich, 1994) and the biophysics of the bodies and nervous systems that send and receive signals (e.g., Aronov & Fee, 2012; Thiessen, 1983b). For example, auditory sensitivity varies significantly with ambient temperature, because of the influence of temperature on multiple components of the auditory system (e.g., cochlea, auditory nerve; see Thiessen, 1983a). Many species thus exhibit a coupling between ambient temperature and communicative signaling and mating frequency (Thiessen, 1983a). In crickets (*Gryllidae*), this coupling is tight enough that the chirping rate of a cricket can be used to estimate ambient temperature (i.e., Dolbear’s law; Dolbear, 1897). In field crickets (*Gryllinae*), females mate more frequently at warmer temperatures (Kindle, Johnson, Ivy, Weddle, & Sakaluk, 2006)

and males, correspondingly, prefer to chirp from warmer locations (and thus at higher rates; Hedrick, Perez, Lichti, & Yew, 2002). Depending on species, females tend to either prefer males who chirp at rates corresponding to their own body temperatures (see Thiessen, 1983b) or else possess broad frequency tuning, spanning the entire range from which males of their species are likely to signal (e.g., Mhatre, Bhattacharya, Robert, & Balakrishnan, 2011). A recent study in zebra finches (*Taeniopygia guttata*) uncovered a similar coupling between temperature and social signaling in that nearly all of the variance in the tempo of male song—relatable to social and circadian context—was explained by variation in brain temperature (Aronov & Fee, 2012).

#### THERMOREGULATION IN DEVELOPMENTAL CONTEXT

Just as different species inhabit distinct ecological niches, animals of different ages, within species, often inhabit radically different energetic and thermoregulatory niches. In these cases, organisms

<sup>11</sup>Many other species show elevations in body or brain temperature during social encounters that are unlikely to be related to chemosensory signaling and are often labeled *emotional hyperthermia* (e.g., Mohammed, Ootsuka, & Blessing, 2014).

often possess adaptations that are specific to a given life stage (i.e., *ontogenetic adaptations*; see Figure 45.2; J. R. Alberts & Harshaw, 2014; Blumberg, 2001; Oppenheim, 1981). Reduced body size compared to adults is among the most significant factors constraining thermoregulation in young organisms. Size can vary even by several orders of magnitude, depending on species. For example, larvae of the Carolina sphinx moth (*Manduca sexta*) increase in size over 10,000 fold during their first few weeks posthatch, leading to dramatic thermoregulatory differences between larvae of different instars (Woods, 2013).

Similarly, newborn rats and mice are small, with much larger surface-to-volume ratios than adults, and are also furless, with little capacity for shivering thermogenesis (Blumberg, 2001; Leon, 1986). The body temperatures of such infants thus fall rapidly if they are isolated and left on their own at cool temperatures. For this reason, infant rodents were historically described as *poikilotherms* and thought to be incapable of adaptive response to thermal challenge. However, such studies involved testing infants in isolation from critical elements of their species-typical niche (see Blumberg, 2001). For example, the nests, burrows, and other structures used by myriad species, including rats and mice, serve to buffer embryos and infants from heat loss when adults are away from the nest. In *multiparous* species, such as mice, rats, rabbits (*Leporidae*), and many birds, infants also huddle vigorously when exposed to cold, reducing their collective heat loss (see J. R. Alberts, 2007; Gilbert et al., 2010). In fact, groups of infant rats and mice exhibit behavior that individual infants are incapable of—expanding and contracting with increases and decreases of ambient temperature, displaying active group regulatory behavior (J. R. Alberts, 1978; Harshaw & Alberts, 2012).

In addition to huddling with nestmates, infant rats and mice—like other mammalian infants—typically have large deposits of BAT, particularly in the interscapular region (i.e., between the shoulders). The size of BAT deposits is greatly enlarged in infants relative to BAT deposits in adults, lending support to the characterization of these large BAT deposits as an ontogenetic adaptation to the early postnatal thermoregulatory niche. That is, these BAT deposits buffer infants from cold

stress experienced early in development, prior to the emergence of the full suite of adult thermoregulatory adaptations (J. R. Alberts & Harshaw, 2014; Blumberg, 2001). Although BAT has traditionally been characterized as an exclusively thermal effector, a number of findings suggest that BAT may have thermoregulatory and social functions, particularly in providing a hotspot—generating a steep thermal gradient—that can function as a target for nestmates seeking warmth. Specifically, Sokoloff and Blumberg (2001) found that groups of infant rats with pharmacologically inactivated BAT huddled far less cohesively when challenged with cold. Moreover, in mixed groups of BAT-active and BAT-inactive pups, BAT-active pups huddled preferentially with each other (Sokoloff & Blumberg, 2001). Similarly, the relative upregulation of BAT in female C57BL/6 mice (a common laboratory strain) was found to result in female pups obtaining significantly more contacts during cold-induced huddling than male siblings (Harshaw, Culligan, & Alberts, 2014). Interestingly, oxytocin—often regarded as the social hormone—is an endogenous *pyrogen* (producer of metabolic heat) that influences multiple components of the homeostatic response to cold, including BAT thermogenesis (Kasahara et al., 2013). Manipulations of the oxytocin system thus impact BAT thermogenesis and huddling cohesiveness in mice (e.g., J. R. Alberts, 2007).

An additional developmental issue is how ambient temperature constrains interactions among parents and offspring (see Chapters 35 and 36, this volume). For example, ambient temperature is negatively correlated with the occurrence of mother–infant ventroventral contact in hamadryas baboons, presumably because of its consequences for heat exchange (Brent, Koban, & Evans, 2003). Ambient temperature also influences the size of nests constructed by pregnant rodents (e.g., Lynch & Possidente, 1978), the timing of incubation bouts in birds (e.g., Conway & Martin, 2000), and care for eggs in stickleback fish (*Gasterosteus aculeatus*; Hopkins, Moss, & Gill, 2011). In rodents, dams greatly increase their metabolic rate to meet pup nutritive requirements and are thus prone to hyperthermia while lactating (e.g., Scribner & Wynne-Edwards, 1994). And although the results

in rats are controversial (see Leon, Coopersmith, Beasley, & Sullivan, 1990; Stern & Azzara, 2002), evidence suggests that, at least under some contexts, maternal body temperature can be a limiting factor for the provisioning of care to pups (e.g., Scribner & Wynne-Edwards, 1994).

The signals emitted by young and responded to by parents can also be temperature dependent. Notably, ultrasonic vocalizations (USVs) produced by infant rodents on separation from the nest (see Chapter 21, this volume), which contribute to pup retrieval by the dam (Farrell & Alberts, 2002), are highly sensitive to temperature (Blumberg & Alberts, 1997; Blumberg & Sokoloff, 2001; Harshaw & Alberts, 2012). Standard procedures for measuring infant USVs involve removing pups from the nest and placing them under isolation at room temperature (20° C–22° C) for 2 to 6 minutes (see Hofer, Shair, & Brunelli, 2002). However, USV production is substantially reduced when pups are isolated under warm ambient conditions and if care is taken to minimize a fall in body temperature during transfer (Blumberg, Efimova, & Alberts, 1992b; 1992a). Although alternative procedures for eliciting USVs that may be more closely related to maternal separation rather than thermal stress have been developed (e.g., Shair, Masmela, Brunelli, & Hofer, 1997), such procedures have not gained widespread adoption and the larger debate on the emotional significance of USVs and the dangers of a too heavily anthropomorphic approach remains largely unsettled (see Blumberg & Sokoloff, 2001; Knutson, Burgdorf, & Panksepp, 2002; see also Chapter 23, this volume).

## WARMTH, THERMOTAXIS, AND LEARNING

As many of the preceding examples illustrate, animals exhibit robust behavioral responses to thermal cues across diverse contexts (Fraenkel & Gunn, 1942). Not surprisingly, when an animal is cold it will generally approach a warm object or location (i.e., show *positive thermotaxis*).<sup>12</sup> This phenomenon can serve as an entry into considerations of warmth as a positive, rewarding stimulus. Beginning in the 1950s, experimentalists explored the function of

warmth as a reinforcing stimulus, most often using operant paradigms. In a seminal study, rats pressed a lever in a small, cold chamber to receive 10 s of warm air delivered through the floor of the apparatus, raising the temperature of the air around them (Weiss & Laties, 1961). In later studies, such convective warming was replaced by radiant heating with infrared lamps, which provided better thermal control and enabled parametric studies in which stimulus intensity and duration were varied under different ambient challenges. There followed similar Pavlovian- and operant-based studies with birds, fish, and reptiles (e.g., Rozin & Mayer, 1961).

Developmental analyses appeared more recently. Flory et al. (1997) rewarded day-old rats with 20 s warming, contingent on the pup turning its head to one side. Pups rapidly learned this response, which extinguished when head turning to the originally correct side was no longer rewarded. Nevertheless, when such learning was studied developmentally (i.e., in 1- to 11-day-old rats) an interesting pattern emerged: Day-old pups learned a reversal of the original response, but older pups did not (Hoffman, Flory, & Alberts, 1999a). Subsequent analyses suggested that it was the newborns' stronger thermotaxic responses that permitted the reversal learning. Hoffman et al. (1999b) took note of the age-related changes in thermotaxis and framed their follow-up investigations in terms of changes in a young mammal's thermal preferences and adaptive learning strategies. In addition to examining learning for warm rewards during cold challenge, they also studied learning for cool rewards during hot challenges. After calibrating the challenges and the reinforcement values, they found that 5- and 10-day-olds could learn to use the head-turning operant response for heating when cold as well as cooling when hot, but the cold stimulus was not as effective a reward with day-old pups. Hoffman et al. (1999b) showed that day-old pups displayed a profound, positive thermotaxis, whereas 5- and 10-day-olds were progressively less taxic on the same thermocline. It thus appeared that the neonate's exaggerated positive thermotaxis compared to older pups was an ontogenetic adaptation.

<sup>12</sup>In some cases, such approach responses can be unregulated in the sense that animals move relentlessly toward heat, even if this entails exposure to dangerously high temperatures.

The roles of thermal stimuli in the learning of social cues have also been studied. Odor learning by young rats and mice is strongly influenced by associations with thermotactile stimulation (see Chapter 21, this volume and Volume 2, Chapter 4, this handbook). This kind of learning was initially identified in studies of olfactory-guided huddling in rat pups. J. R. Alberts and May (1984) implemented a regime of exposures in which experimental odors were paired with different forms of maternal care or elements of maternal care. Preference in choice tests for huddling with scented surrogates (tubes wrapped with acrylic fur) was used as a measure of learning. Potential sources of reinforcement, such as mother's milk, maternal licking, or perioral stimulation from suckling were found to be either unnecessary or ineffective for this form of odor preference learning. The key element for reinforcement was conductive heat exchange, as evidenced by the efficacy of a warm furry tube as the maternal stimulus that induced the huddling preference (J. R. Alberts & May, 1984). More recently, this procedure was refined and simplified, providing the opportunity to investigate neuroendocrine modulation of learning during huddling (Kojima & Alberts, 2009). Specifically, nonnutritive, thermotactile stimulation was not only associated with higher levels of hypothalamic oxytocin, but the resultant odor learning was found to be mediated by oxytocin neurons, as it was blocked by intraventricular injection of an oxytocin receptor antagonist (Kojima & Alberts, 2011). Thus, it appears that neuropeptide circuits, known to support a variety of social behaviors, are highly responsive to thermal cues and may depend on them for establishing some fundamental social preferences.

## CONCLUSION AND FUTURE DIRECTIONS

Temperature has a pervasive influence on physiology and behavior—a fact that is perhaps easily forgotten in the context of model species studied under highly controlled laboratory conditions (see Maloney et al., 2014; Messmer et al., 2014). The niches that organisms inhabit and within which they develop and evolve are characterized by myriad thermal and energetic constraints,

many of these—outside of the laboratory—driven by the nested daily and seasonal cyclicities inherent in the terrestrial ecosystem. The interaction of the size, shape, structure, and metabolism of the organism with the physical and social environment is key to identifying and understanding thermoregulatory constraints as well as to making meaningful comparisons between species (e.g., Maloney et al., 2014; Speakman, 2013). As we have illustrated, organisms show myriad and diverse adaptations—morphological, physiological, and behavioral—in the face of such constraints. These are tied closely to the climates and ecosystems within which animals find themselves and often vary as a function of social context and over the course of development (Allee, 1938; Blumberg, 2001).

Many emerging research domains stand to benefit from a comparative understanding of thermoregulation. For example, there is growing interest in the relevance of mitochondrial functioning, neural bioenergetics, and brain temperature to cognitive functioning in disorders ranging from mitochondrial disease, to autism, Parkinson's disease, and depression (e.g., Rango et al., 2014; Klinedinst & Regenold, 2015). There is also growing interest in the effects of climate change (i.e., global warming) on physiology, behavior, and survival. This includes understanding the effects of temperature change on phenotypic development (e.g., Seebacher & Grigaltchik, 2015), how rising temperatures may exacerbate neurobehavioral toxicity of anthropogenic contaminants (e.g., Little & Seebacher, 2015), and whether and to what extent behavior may, in cases, mitigate deleterious consequences of such change (e.g., McFarland, Barrett, Boner, Freeman, & Henzi, 2014; Rojas et al., 2014). Given the wide range of behaviors and phenotypes known to be sensitive to ambient temperature (e.g., social behavior, parental care, obesity, sleep, aggression, susceptibility to cancer), climate change can be predicted to bring many and varied consequences for wild populations. Some of these may nevertheless be more drastic or easily observable, at least initially, for ectotherms than endotherms (e.g., on dispersal; Sheldon, Yang, & Tewksbury, 2011). For example, in reptiles and amphibians, the ambient temperature experienced prenatally can significantly affect not

only the overall rate of development and viability of the embryo but also a range of phenotypes of critical importance for fitness and survival, including sex determination, mate-choice, and, vulnerability to predation (e.g., Putz & Crews, 2006; Seebacher & Grigaltchik, 2015). By the same token, climate change may affect a given species more drastically during particularly ontogenetic phases, depending on the details of life history, growth trajectory, and so forth (see Huey et al., 2012).

Mechanistic understanding of these questions will thus require careful comparative work and animal modeling (e.g., Naviaux et al., 2015), with close attention paid to species-, age- and context-specific differences in thermoregulatory and metabolic phenotypes. As recent evidence shows, many experimental manipulations—including those resulting in thermoregulatory and metabolic “deficits”—have observable phenotypic consequences only in the context of specific ambient temperatures (e.g., Cannon & Nedergaard, 2011). At the same time, alterations of temperature have numerous consequences for brain and behavior that hinge critically on the fine details of social, developmental, and physical context (Kiyatkin, 2014). Comparative psychologists have the potential to play a critical role in exploring these and many other issues related to animal behavior in our diverse and changing thermal world.

## References

- Alberts, A. C. (1992). Constraints on the design of chemical communication systems in terrestrial vertebrates. *American Naturalist*, *139*, S62–S89. <http://dx.doi.org/10.1086/285305>
- Alberts, J. R. (1978). Huddling by rat pups: Group behavioral mechanisms of temperature regulation and energy conservation. *Journal of Comparative and Physiological Psychology*, *92*, 231–245. <http://dx.doi.org/10.1037/h0077459>
- Alberts, J. R. (2007). Huddling by rat pups: Ontogeny of individual and group behavior. *Developmental Psychobiology*, *49*, 22–32. <http://dx.doi.org/10.1002/dev.20190>
- Alberts, J. R., & Gubernick, D. (1983). Reciprocity and resource exchange: A symbiotic model of parent–offspring relations. In L. Rosenblum (Ed.), *Symbiosis in parent–offspring interactions* (pp. 7–44). [http://dx.doi.org/10.1007/978-1-4684-4565-7\\_2](http://dx.doi.org/10.1007/978-1-4684-4565-7_2)
- Alberts, J. R., & Harshaw, C. (2014). Behavioral development and ontogenetic adaptation. In K. Yasukawa & Z. Tang-Martinez (Eds.), *Animal behavior: How and why animals do the things they do* (Vol. 1, pp. 289–324). Westport, CT: Praeger.
- Alberts, J. R., & May, B. (1984). Nonnutritive, thermotactile induction of filial huddling in rat pups. *Developmental Psychobiology*, *17*, 161–181. <http://dx.doi.org/10.1002/dev.420170207>
- Allee, W. C. (1931). *Animal aggregations: A study in general sociology*. <http://dx.doi.org/10.5962/bhl.title.7313>
- Allee, W. C. (1934). Recent studies in mass physiology. *Biological Reviews of the Cambridge Philosophical Society*, *9*, 1–48. <http://dx.doi.org/10.1111/j.1469-185X.1934.tb00872.x>
- Allee, W. C. (1938). *The social life of animals*. <http://dx.doi.org/10.5962/bhl.title.7226>
- Anderson, J. R. (1984). Ethology and ecology of sleep in monkeys and apes. *Advances in the Study of Behavior*, *14*, 165–229. [http://dx.doi.org/10.1016/S0065-3454\(08\)60302-2](http://dx.doi.org/10.1016/S0065-3454(08)60302-2)
- Andervont, H. B. (1944). Influence of environment on mammary cancer in mice. *Journal of the National Cancer Institute*, *4*, 579–581.
- Argyropoulos, G., & Harper, M. E. (2002). Uncoupling proteins and thermoregulation. *Journal of Applied Physiology*, *92*, 2187–2198. <http://dx.doi.org/10.1152/jappphysiol.00994.2001>
- Aronov, D., & Fee, M. S. (2012). Natural changes in brain temperature underlie variations in song tempo during a mating behavior. *PLOS ONE*, *7*, e47856–e47856. <http://dx.doi.org/10.1371/journal.pone.0047856>
- Balter, M. (2014). Dinosaur metabolism neither hot nor cold, but just right. *Science*, *344*, 1216–1217. <http://dx.doi.org/10.1126/science.344.6189.1216>
- Bara, M., & Guiet-Bara, A. (1986). Temperature effect on ion transport through the isolated human amnion: Part I. Electrophysiological studies. *Bioelectrochemistry and Bioenergetics*, *15*, 383–394. [http://dx.doi.org/10.1016/0302-4598\(86\)85026-7](http://dx.doi.org/10.1016/0302-4598(86)85026-7)
- Bartolini, T., Butail, S., & Porfiri, M. (2015). Temperature influences sociality and activity of freshwater fish. *Environmental Biology of Fishes*, *98*, 825–832. <http://dx.doi.org/10.1007/s10641-014-0318-8>
- Beach, F. A. (1950). The snark was a boojum. *American Psychologist*, *5*, 115–124. <http://dx.doi.org/10.1037/h0056510>
- Berger, R. J., & Phillips, N. H. (1993). Sleep and energy conservation. *Physiology*, *8*, 276–281.
- Blessing, W., Mohammed, M., & Ootsuka, Y. (2012). Heating and eating: Brown adipose tissue

- thermogenesis precedes food ingestion as part of the ultradian basic rest-activity cycle in rats. *Physiology and Behavior*, *105*, 966–974. <http://dx.doi.org/10.1016/j.physbeh.2011.11.009>
- Blessing, W., Mohammed, M., & Ootsuka, Y. (2013). Brown adipose tissue thermogenesis, the basic rest-activity cycle, meal initiation, and bodily homeostasis in rats. *Physiology and Behavior*, *121*, 61–69. <http://dx.doi.org/10.1016/j.physbeh.2013.03.028>
- Blumberg, M. S. (2001). The developmental context of thermal homeostasis. In E. M. Blass (Ed.), *Handbook of behavioral neurobiology* (Vol. 13, pp. 199–228). New York, NY: Kluwer Academic/Plenum Press.
- Blumberg, M. S. (2002). *Body heat: Temperature and life on earth*. Cambridge, MA: Harvard University Press.
- Blumberg, M. S. (2015). Developing sensorimotor systems in our sleep. *Current Directions in Psychological Science*, *24*, 32–37. <http://dx.doi.org/10.1177/0963721414551362>
- Blumberg, M. S., & Alberts, J. R. (1997). Incidental emissions, fortuitous effects, and the origins of communication. *Perspectives in Ethology*, *12*, 225–249. [http://dx.doi.org/10.1007/978-1-4899-1745-4\\_8](http://dx.doi.org/10.1007/978-1-4899-1745-4_8)
- Blumberg, M. S., Efimova, I. V., & Alberts, J. R. (1992a). Thermogenesis during ultrasonic vocalization by rat pups isolated in a warm environment: A thermographic analysis. *Developmental Psychobiology*, *25*, 497–510. <http://dx.doi.org/10.1002/dev.420250704>
- Blumberg, M. S., Efimova, I. V., & Alberts, J. R. (1992b). Ultrasonic vocalizations by rat pups: The primary importance of ambient temperature and the thermal significance of contact comfort. *Developmental Psychobiology*, *25*, 229–250. <http://dx.doi.org/10.1002/dev.420250402>
- Blumberg, M. S., & Sokoloff, G. (2001). Do infant rats cry? *Psychological Review*, *108*, 83–95. <http://dx.doi.org/10.1037/0033-295X.108.1.83>
- Blumberg, M. S., & Stolba, M. A. (1996). Thermogenesis, myoclonic twitching, and ultrasonic vocalization in neonatal rats during moderate and extreme cold exposure. *Behavioral Neuroscience*, *110*, 305–314. <http://dx.doi.org/10.1037/0735-7044.110.2.305>
- Bogert, C. M. (1949). Thermoregulation in reptiles; a factor in evolution. *Evolution: International Journal of Organic Evolution*, *3*, 195–211. <http://dx.doi.org/10.2307/2405558>
- Boily, P. (1995). Theoretical heat flux in water and habitat selection of phocid seals and beluga whales during the annual molt. *Journal of Theoretical Biology*, *172*, 235–244. <http://dx.doi.org/10.1006/jtbi.1995.0020>
- Boratyński, J. S., Willis, C. K. R., Jefimow, M., & Wojciechowski, M. S. (2015). Huddling reduces evaporative water loss in torpid Natterer's bats, *Myotis nattereri*. *Comparative Biochemistry and Physiology, Part A*, *179*, 125–132.
- Boyles, J. G., Thompson, A. B., McKechnie, A. E., Malan, E., Humphries, M. M., & Careau, V. (2013). A global heterothermic continuum in mammals. *Global Ecology and Biogeography*, *22*, 1029–1039. <http://dx.doi.org/10.1111/geb.12077>
- Brain, C., & Mitchell, D. (1999). Body temperature changes in free-ranging baboons (*Papio hamadryas ursinus*) in the Namib Desert, Namibia. *International Journal of Primatology*, *20*, 585–598. <http://dx.doi.org/10.1023/A:1020394824547>
- Branco, L. G., Gargaglioni, L. H., & Barros, R. C. (2006). Anapnoea during hypoxia. *Journal of Thermal Biology*, *31*, 82–89. <http://dx.doi.org/10.1016/j.jtherbio.2005.11.020>
- Brent, L., Koban, T., & Evans, S. (2003). The influence of temperature on the behavior of captive mother–infant baboons. *Behaviour*, *140*, 209–224. <http://dx.doi.org/10.1163/156853903321671505>
- Brischoux, F., Bonnet, X., & Shine, R. (2009). Kleptothermy: An additional category of thermoregulation, and a possible example in sea kraits (*Laticauda laticaudata*, *Serpentes*). *Biology Letters*, *5*, 729–731. <http://dx.doi.org/10.1098/rsbl.2009.0550>
- Briscoe, N. J., Handasyde, K. A., Griffiths, S. R., Porter, W. P., Krockenberger, A., & Kearney, M. R. (2014). Tree-hugging koalas demonstrate a novel thermoregulatory mechanism for arboreal mammals. *Biology Letters*, *10*, 235. <http://dx.doi.org/10.1098/rsbl.2014.0235>
- Brown, P. L., & Kiyatkin, E. A. (2004). Brain hyperthermia induced by MDMA (ecstasy): Modulation by environmental conditions. *European Journal of Neuroscience*, *20*, 51–58. <http://dx.doi.org/10.1111/j.0953-816X.2004.03453.x>
- Burghardt, G. M. (1988). Precocity, play, and the ectotherm-endotherm transition: Profound reorganization or superficial adaptation? In E. M. Blass (Ed.), *Developmental psychobiology and behavioral ecology* (pp. 107–148). [http://dx.doi.org/10.1007/978-1-4684-5421-5\\_4](http://dx.doi.org/10.1007/978-1-4684-5421-5_4)
- Canals, M., Rosenmann, M., & Bozinovic, F. (1989). Energetics and geometry of huddling in small mammals. *Journal of Theoretical Biology*, *141*, 181–189. [http://dx.doi.org/10.1016/S0022-5193\(89\)80016-5](http://dx.doi.org/10.1016/S0022-5193(89)80016-5)
- Cannon, B., & Nedergaard, J. (2004). Brown adipose tissue: Function and physiological significance. *Physiological Reviews*, *84*, 277–359. <http://dx.doi.org/10.1152/physrev.00015.2003>

- Cannon, B., & Nedergaard, J. (2010). Metabolic consequences of the presence or absence of the thermogenic capacity of brown adipose tissue in mice (and probably in humans). *International Journal of Obesity*, *34*(Suppl. 1), S7–S16. <http://dx.doi.org/10.1038/ijo.2010.177>
- Cannon, B., & Nedergaard, J. (2011). Nonshivering thermogenesis and its adequate measurement in metabolic studies. *Journal of Experimental Biology*, *214*, 242–253. <http://dx.doi.org/10.1242/jeb.050989>
- Careau, V., Killen, S. S., & Metcalfe, N. B. (2015). Adding fuel to the “fire of life”: Energy budgets across levels of variation in ectotherms and endotherms. In L. B. Martin, C. K. Ghalambor, & A. Woods (Eds.), *Integrative organismal biology* (pp. 219–233). New York, NY: Wiley.
- Carey, F. G. (1982). A brain heater in the swordfish. *Science*, *216*, 1327–1329. <http://dx.doi.org/10.1126/science.7079766>
- Cirelli, C., Gutierrez, C. M., & Tononi, G. (2004). Extensive and divergent effects of sleep and wakefulness on brain gene expression. *Neuron*, *41*, 35–43. [http://dx.doi.org/10.1016/S0896-6273\(03\)00814-6](http://dx.doi.org/10.1016/S0896-6273(03)00814-6)
- Clarke, A. (1991). Cold adaptation. *Journal of Zoology*, *225*, 691–699. <http://dx.doi.org/10.1111/j.1469-7998.1991.tb04339.x>
- Conway, C. J., & Martin, T. E. (2000). Effects of ambient temperature on avian incubation behavior. *Behavioral Ecology*, *11*, 178–188. <http://dx.doi.org/10.1093/beheco/11.2.178>
- Cryan, P. M., & Wolf, B. O. (2003). Sex differences in the thermoregulation and evaporative water loss of a heterothermic bat, *Lasiurus cinereus*, during its spring migration. *Journal of Experimental Biology*, *206*, 3381–3390. <http://dx.doi.org/10.1242/jeb.00574>
- Davenport, J. (1992). Anatomy and physiology of endotherms. *Animal Life at Low Temperature* (pp. 88–109). [http://dx.doi.org/10.1007/978-94-011-2344-0\\_4](http://dx.doi.org/10.1007/978-94-011-2344-0_4)
- Dawson, N. J., & Keber, A. W. (1979). Physiology of heat loss from an extremity: The tail of the rat. *Clinical and Experimental Pharmacology and Physiology*, *6*, 69–80. <http://dx.doi.org/10.1111/j.1440-1681.1979.tb00009.x>
- Dee Boersma, P. (1982). The benefits of sleeping aggregations in marine iguanas, *Amblyrhynchus cristatus*. In G. M. Burghardt & A. S. Rand (Eds.), *Iguanas of the world: Their behavior, ecology, and conservation* (pp. 292–299). New York, NY: Noyes.
- Dolbear, A. E. (1897). The cricket as a thermometer. *American Naturalist*, *31*, 970–971. <http://dx.doi.org/10.1086/276739>
- Enerbäck, S., Jacobsson, A., Simpson, E. M., Guerra, C., Yamashita, H., Harper, M. E., & Kozak, L. P. (1997). Mice lacking mitochondrial uncoupling protein are cold-sensitive but not obese. *Nature*, *387*, 90–94. <http://dx.doi.org/10.1038/387090a0>
- Eng, J. W.-L., Reed, C. B., Kokolus, K. M., Pitoniak, R., Utley, A., Bucsek, M. J., . . . Hylander, B. L. (2015). Housing temperature-induced stress drives therapeutic resistance in murine tumour models through  $\beta$ 2-adrenergic receptor activation. *Nature Communications*, *6*, 6426–6426. <http://dx.doi.org/10.1038/ncomms7426>
- Farrell, W. J., & Alberts, J. R. (2002). Maternal responsiveness to infant Norway rat (*Rattus norvegicus*) ultrasonic vocalizations during the maternal behavior cycle and after steroid and experiential induction regimens. *Journal of Comparative Psychology*, *116*, 286–296. <http://dx.doi.org/10.1037/0735-7036.116.3.286>
- Feldmann, H. M., Golozoubova, V., Cannon, B., & Nedergaard, J. (2009). UCP1 ablation induces obesity and abolishes diet-induced thermogenesis in mice exempt from thermal stress by living at thermoneutrality. *Cell Metabolism*, *9*, 203–209. <http://dx.doi.org/10.1016/j.cmet.2008.12.014>
- Flory, G. S., Langley, C. M., Pfister, J. F., & Alberts, J. R. (1997). Instrumental learning for a thermal reinforcer in 1-day-old rats. *Developmental Psychobiology*, *30*, 41–47. [http://dx.doi.org/10.1002/\(SICI\)1098-2302\(199701\)30:1<41::AID-DEV4>3.0.CO;2-V](http://dx.doi.org/10.1002/(SICI)1098-2302(199701)30:1<41::AID-DEV4>3.0.CO;2-V)
- Fraenkel, G. S., & Gunn, D. L. (1942). *The orientation of animals*. New York, NY: Dover.
- Gaskill, B. N., Gordon, C. J., Pajor, E. A., Lucas, J. R., Davis, J. K., & Garner, J. P. (2012). Heat or insulation: Behavioral titration of mouse preference for warmth or access to a nest. *PLOS ONE*, *7*, e32799. <http://dx.doi.org/10.1371/journal.pone.0032799>
- Gaskill, B. N., Rohr, S. A., Pajor, E. A., Lucas, J. R., & Garner, J. P. (2009). Some like it hot: Mouse temperature preferences in laboratory housing. *Applied Animal Behaviour Science*, *116*, 279–285. <http://dx.doi.org/10.1016/j.applanim.2008.10.002>
- Gaskill, B. N., Rohr, S. A., Pajor, E. A., Lucas, J. R., & Garner, J. P. (2011). Working with what you've got: Changes in thermal preference and behavior in mice with or without nesting material. *Journal of Thermal Biology*, *36*, 193–199. <http://dx.doi.org/10.1016/j.jtherbio.2011.02.004>
- Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annual Review of Physiology*, *66*, 239–274. <http://dx.doi.org/10.1146/annurev.physiol.66.032102.115105>
- Gilbert, C., McCafferty, D., Le Maho, Y., Martrette, J.-M., Giroud, S., Blanc, S., & Ancel, A. (2010). One for all and all for one: The energetic benefits of huddling



- in endotherms. *Biological Reviews of the Cambridge Philosophical Society*, 85, 545–569.
- Gillooly, J. F., & Ophir, A. G. (2010). The energetic basis of acoustic communication. *Proceedings of the Royal Society: Series B, Biological Sciences*, 277, 1325–1331. <http://dx.doi.org/10.1098/rspb.2009.2134>
- Gisolfi, C. V., & Mora, F. (2000). *The hot brain: Survival, temperature, and the human body*. Cambridge, MA: MIT Press
- Golozoubova, V., Hohtola, E., Matthias, A., Jacobsson, A., Cannon, B., & Nedergaard, J. (2001). Only UCPI can mediate adaptive nonshivering thermogenesis in the cold. *FASEB Journal*, 15, 2048–2050.
- Gordon, C. J. (1994). 24-hour control of body temperature in rats. I. Integration of behavioral and autonomic effectors. *American Journal of Physiology*, 267, R71–R77.
- Gordon, C. J. (2004). Effect of cage bedding on temperature regulation and metabolism of group-housed female mice. *Comparative Medicine*, 54, 63–68.
- Gordon, C. J., Becker, P., & Ali, J. S. (1998). Behavioral thermoregulatory responses of single- and group-housed mice. *Physiology and Behavior*, 65, 255–262. [http://dx.doi.org/10.1016/S0031-9384\(98\)00148-6](http://dx.doi.org/10.1016/S0031-9384(98)00148-6)
- Gordon, C. J., & Rowsey, P. J. (2009). The influence of temperature on toxicity. In B. Ballantyne, T. Marrs, & T. Syversen (Eds.), *General, applied, and systems toxicology* (pp. 643–658). <http://dx.doi.org/10.1002/9780470744307.gat032>
- Gottlieb, G., & Lickliter, R. (2004). The various roles of animal models in understanding human development. *Social Development*, 13, 311–325. <http://dx.doi.org/10.1111/j.1467-9507.2004.000269.x>
- Gould, S. J. (1966). Allometry and size in ontogeny and phylogeny. *Biological Reviews of the Cambridge Philosophical Society*, 41, 587–638. <http://dx.doi.org/10.1111/j.1469-185X.1966.tb01624.x>
- Grady, J. M., Enquist, B. J., Dettweiler-Robinson, E., Wright, N. A., & Smith, F. A. (2014). Dinosaur physiology: Evidence for mesothermy in dinosaurs. *Science*, 344, 1268–1272. <http://dx.doi.org/10.1126/science.1253143>
- Greenberg, G. (1972). The effects of ambient temperature and population density on aggression in two inbred strains of mice, *Mus musculus*. *Behaviour*, 42, 119–130. <http://dx.doi.org/10.1163/156853972X00130>
- Harrison, G. F., & Hewitt, D. (1978). The influence of the conventional microflora on the body temperature of the chick. *British Poultry Science*, 19, 273–275. <http://dx.doi.org/10.1080/00071667808416475>
- Harshaw, C., & Alberts, J. R. (2012). Group and individual regulation of physiology and behavior: A behavioral, thermographic, and acoustic study of mouse development. *Physiology and Behavior*, 106, 670–682. <http://dx.doi.org/10.1016/j.physbeh.2012.05.002>
- Harshaw, C., Culligan, J. J., & Alberts, J. R. (2014). Sex differences in thermogenesis structure behavior and contact within huddles of infant mice. *PLOS ONE*, 9, e87405. <http://dx.doi.org/10.1371/journal.pone.0087405>
- Hashimoto, O., Ohtsuki, H., Kakizaki, T., Amou, K., Sato, R., Doi, S., . . . Endo, H. (2015). Brown adipose tissue in cetacean blubber. *PLOS ONE*, 10, e0116734–e0116734. <http://dx.doi.org/10.1371/journal.pone.0116734>
- Haynie, D. T. (2001). *Biological thermodynamics*. <http://dx.doi.org/10.1017/CBO9780511754784>
- Hazel, J. R. (1995). Thermal adaptation in biological membranes: Is homeoviscous adaptation the explanation? *Annual Review of Physiology*, 57, 19–42. <http://dx.doi.org/10.1146/annurev.ph.57.030195.000315>
- Hedrick, A. V., Perez, D., Lichti, N., & Yew, J. (2002). Temperature preferences of male field crickets (*Gryllus integer*) alter their mating calls. *Journal of Comparative Physiology. A, Neuroethology, Sensory, Neural, and Behavioral Physiology*, 188, 799–805. <http://dx.doi.org/10.1007/s00359-002-0368-9>
- Heinrich, B. (1981). Energetics of honeybee swarm thermoregulation. *Science*, 212, 565–566. <http://dx.doi.org/10.1126/science.212.4494.565>
- Heinrich, B. (1993). *The hot-blooded insects*. Cambridge, MA: Harvard University Press.
- Heller, H. C. (2005). Temperature, thermoregulation, and sleep. In M. H. Kryger, T. Roth, & W. C. Dement (Eds.), *Principles and practice of sleep medicine* (pp. 292–304). <http://dx.doi.org/10.1016/B0-72-160797-7/50031-8>
- Hemingway, A. (1963). Shivering. *Physiological Reviews*, 43, 397–422.
- Hetem, R. S., Maloney, S. K., Fuller, A., & Mitchell, D. (2016). Heterothermy in large mammals: Inevitable or implemented? *Biological Reviews of the Cambridge Philosophical Society*, 91, 187–205. <http://dx.doi.org/10.1111/brv.12166>
- Hill, R. A. (2006). Thermal constraints on activity scheduling and habitat choice in baboons. *American Journal of Physical Anthropology*, 129, 242–249. <http://dx.doi.org/10.1002/ajpa.20264>
- Hofer, M. A., Shair, H. N., & Brunelli, S. A. (2002). Ultrasonic vocalizations in rat and mouse pups. *Current Protocols in Neuroscience*, Unit 8.14. <http://dx.doi.org/10.1002/0471142301.ns0814s17>

- Hoffman, C. M., Flory, G. S., & Alberts, J. R. (1999a). Neonatal thermotaxis improves reversal of a thermally reinforced operant response. *Developmental Psychobiology*, *34*, 87–99. [http://dx.doi.org/10.1002/\(SICI\)1098-2302\(199903\)34:2<87::AID-DEV2>3.0.CO;2-W](http://dx.doi.org/10.1002/(SICI)1098-2302(199903)34:2<87::AID-DEV2>3.0.CO;2-W)
- Hoffman, C. M., Flory, G. S., & Alberts, J. R. (1999b). Ontogenetic adaptation and learning: A developmental constraint in learning for a thermal reinforcer. *Developmental Psychobiology*, *34*, 73–86. [http://dx.doi.org/10.1002/\(SICI\)1098-2302\(199903\)34:2<73::AID-DEV1>3.0.CO;2-B](http://dx.doi.org/10.1002/(SICI)1098-2302(199903)34:2<73::AID-DEV1>3.0.CO;2-B)
- Hopkins, K., Moss, B. R., & Gill, A. B. (2011). Increased ambient temperature alters the parental care behaviour and reproductive success of the three-spined stickleback (*Gasterosteus aculeatus*). *Environmental Biology of Fishes*, *90*, 121–129. <http://dx.doi.org/10.1007/s10641-010-9724-8>
- Houser, D. S., Crocker, D. E., & Costa, D. P. (2005). Ecology of water relations and thermoregulation. *eLS*. <http://dx.doi.org/10.1038/npg.els.0003216>
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A., Jess, M., & Williams, S. E. (2012). Predicting organismal vulnerability to climate warming: Roles of behaviour, physiology and adaptation. *Philosophical Transactions of the Royal Society: Series B, Biological Sciences*, *367*, 1665–1679. <http://dx.doi.org/10.1098/rstb.2012.0005>
- Ito, K. (1999). Isolation of two distinct cold-inducible cDNAs encoding plant uncoupling proteins from the spadix of skunk cabbage (*Symplocarpus foetidus*). *Plant Science*, *149*, 167–173. [http://dx.doi.org/10.1016/S0168-9452\(99\)00159-4](http://dx.doi.org/10.1016/S0168-9452(99)00159-4)
- Kasahara, Y., Sato, K., Takayanagi, Y., Mizukami, H., Ozawa, K., Hidema, S., . . . Nishimori, K. (2013). Oxytocin receptor in the hypothalamus is sufficient to rescue normal thermoregulatory function in male oxytocin receptor knockout mice. *Endocrinology*, *154*, 4305–4315. <http://dx.doi.org/10.1210/en.2012-2206>
- Kindle, T. K., Johnson, K. M., Ivy, T. M., Weddle, C. B., & Sakaluk, S. K. (2006). Female mating frequency increases with temperature in two cricket species, *Grylloides sigillatus* and *Acheta domesticus* (Orthoptera: Gryllidae). *Canadian Journal of Zoology*, *84*, 1345–1350. <http://dx.doi.org/10.1139/z06-127>
- Kingma, B. R., Frijns, A. J., Schellen, L., & van Marken Lichtenbelt, W. D. (2014). Beyond the classic thermoneutral zone. *Temperature*, *1*, 142–149. <http://dx.doi.org/10.4161/temp.29702>
- Kiyatkin, E. A. (2010). Brain temperature homeostasis: Physiological fluctuations and pathological shifts. *Frontiers in Bioscience*, *15*, 73–92. <http://dx.doi.org/10.2741/3608>
- Kiyatkin, E. A. (2014). State-dependent and environmental modulation of brain hyperthermic effects of psychoactive drugs of abuse. *Temperature*, *1*, 201–213. <http://dx.doi.org/10.4161/23328940.2014.969074>
- Kiyatkin, E. A., & Sharma, H. S. (2009). Permeability of the blood-brain barrier depends on brain temperature. *Neuroscience*, *161*, 926–939. <http://dx.doi.org/10.1016/j.neuroscience.2009.04.004>
- Klinedinst, N. J., & Regenold, W. T. (2015). A mitochondrial bioenergetic basis of depression. *Journal of Bioenergetics and Biomembranes*, *47*, 155–171.
- Kluger, M. J. (1979). Fever in ectotherms: Evolutionary implications. *American Zoologist*, *19*, 295–304. <http://dx.doi.org/10.1093/icb/19.1.295>
- Kluger, M. J., Conn, C. A., Franklin, B., Freter, R., & Abrams, G. D. (1990). Effect of gastrointestinal flora on body temperature of rats and mice. *American Journal of Physiology*, *258*, R552–R557.
- Kluger, M. J., Kozak, W., Conn, C. A., Leon, L. R., & Soszynski, D. (1998). Role of fever in disease. *Annals of the New York Academy of Sciences*, *856*, 224–233. <http://dx.doi.org/10.1111/j.1749-6632.1998.tb08329.x>
- Knutson, B., Burgdorf, J., & Panksepp, J. (2002). Ultrasonic vocalizations as indices of affective states in rats. *Psychological Bulletin*, *128*, 961–977. <http://dx.doi.org/10.1037/0033-2909.128.6.961>
- Kojima, S., & Alberts, J. R. (2009). Maternal care can rapidly induce an odor-guided huddling preference in rat pups. *Developmental Psychobiology*, *51*, 95–105. <http://dx.doi.org/10.1002/dev.20349>
- Kojima, S., & Alberts, J. R. (2011). Oxytocin mediates the acquisition of filial, odor-guided huddling for maternally-associated odor in preweaning rats. *Hormones and Behavior*, *60*, 549–558. <http://dx.doi.org/10.1016/j.yhbeh.2011.08.003>
- Kokulus, K. M., Capitano, M. L., Lee, C.-T., Eng, J. W.-L., Waight, J. D., Hylander, B. L., . . . Repasky, E. A. (2013). Baseline tumor growth and immune control in laboratory mice are significantly influenced by subthermoneutral housing temperature. *Proceedings of the National Academy of Sciences, USA*, *110*, 20176–20181. <http://dx.doi.org/10.1073/pnas.1304291110>
- Kokulus, K. M., Spangler, H. M., Povinelli, B. J., Farren, M. R., Lee, K. P., & Repasky, E. A. (2014). Stressful presentations: Mild cold stress in laboratory mice influences phenotype of dendritic cells in naive and tumor-bearing mice. *Frontiers in Immunology*, *5*, 23–23. <http://dx.doi.org/10.3389/fimmu.2014.00023>
- Laursen, W. J., Mastrotto, M., Pesta, D., Funk, O. H., Goodman, J. B., Merriman, D. K., . . . Gracheva, E. O. (2015). Neuronal UCPI expression suggests a mechanism for local thermogenesis during hibernation. *Proceedings of the National*

- Academy of Sciences, USA, 112, 1607–1612. <http://dx.doi.org/10.1073/pnas.1421419112>
- Lawrence, C. (2007). The husbandry of zebrafish (*Danio rerio*): A review. *Aquaculture*, 269, 1–20. <http://dx.doi.org/10.1016/j.aquaculture.2007.04.077>
- Leon, M. (1986). Development of thermoregulation. In E. M. Blass (Ed.), *Developmental psychobiology and developmental neurobiology* (pp. 297–322). New York, NY: Plenum Press.
- Leon, M., Coopersmith, R., Beasley, L. J., & Sullivan, R. M. (1990). Thermal aspects of parenting. In N. A. Krasnegor & R. S. Bridges (Eds.), *Mammalian parenting: Biochemical, neurobiological, and behavioral determinants* (pp. 400–415). New York, NY: Oxford University Press.
- Li, D., Ren, B., Grueter, C. C., Li, B., & Li, M. (2010). Nocturnal sleeping habits of the Yunnan snub-nosed monkey in Xiangguqing, China. *American Journal of Primatology*, 72, 1092–1099. <http://dx.doi.org/10.1002/ajp.20871>
- Lillywhite, H. B., & Stein, B. R. (1987). Surface sculpturing and water retention of elephant skin. *Journal of Zoology*, 211, 727–734. <http://dx.doi.org/10.1111/j.1469-7998.1987.tb04483.x>
- Little, A. G., & Seebacher, F. (2015). Temperature determines toxicity: Bisphenol A reduces thermal tolerance in fish. *Environmental Pollution*, 197, 84–89. <http://dx.doi.org/10.1016/j.envpol.2014.12.003>
- Lynch, C. B., & Possidente, B. P., Jr. (1978). Relationships of maternal nesting to thermoregulatory nesting in house mice (*Mus musculus*) at warm and cold temperatures. *Animal Behaviour*, 26, 1136–1143. [http://dx.doi.org/10.1016/0003-3472\(78\)90103-3](http://dx.doi.org/10.1016/0003-3472(78)90103-3)
- Majolo, B., McFarland, R., Young, C., & Qarro, M. (2013). The effect of climatic factors on the activity budgets of Barbary macaques (*Macaca sylvanus*). *International Journal of Primatology*, 34, 500–514. <http://dx.doi.org/10.1007/s10764-013-9678-8>
- Maloney, S. K., Fuller, A., Mitchell, D., Gordon, C., & Overton, J. M. (2014). Translating animal model research: Does it matter that our rodents are cold? *Physiology (Bethesda, MD)*, 29, 413–420. <http://dx.doi.org/10.1152/physiol.00029.2014>
- Marras, S., Killen, S. S., Lindström, J., McKenzie, D. J., Steffensen, J. F., & Domenici, P. (2015). Fish swimming in schools save energy regardless of their spatial position. *Behavioral Ecology and Sociobiology*, 69, 219–226. <http://dx.doi.org/10.1007/s00265-014-1834-4>
- Mathot, K. J., & Dingemanse, N. J. (2015). Energetics and behavior: Unrequited needs and new directions. *Trends in Ecology and Evolution*, 30, 199–206. <http://dx.doi.org/10.1016/j.tree.2015.01.010>
- McFarland, R., Barrett, L., Boner, R., Freeman, N. J., & Henzi, S. P. (2014). Behavioral flexibility of vervet monkeys in response to climatic and social variability. *American Journal of Physical Anthropology*, 154, 357–364. <http://dx.doi.org/10.1002/ajpa.22518>
- McFarland, R., Fuller, A., Hetem, R. S., Mitchell, D., Maloney, S. K., Henzi, S. P., & Barrett, L. (2015). Social integration confers thermal benefits in a gregarious primate. *Journal of Animal Ecology*, 84, 871–878. <http://dx.doi.org/10.1111/1365-2656.12329>
- McFarland, R., & Majolo, B. (2013). Coping with the cold: Predictors of survival in wild Barbary macaques, *Macaca sylvanus*. *Biology Letters*, 9, 20130428–20130428. <http://dx.doi.org/10.1098/rsbl.2013.0428>
- Messmer, M. N., Kokolus, K. M., Eng, J. W.-L., Abrams, S. I., & Repasky, E. A. (2014). Mild cold-stress depresses immune responses: Implications for cancer models involving laboratory mice. *BioEssays*, 36, 884–891. <http://dx.doi.org/10.1002/bies.201400066>
- Mhatre, N., Bhattacharya, M., Robert, D., & Balakrishnan, R. (2011). Matching sender and receiver: Poikilothermy and frequency tuning in a tree cricket. *Journal of Experimental Biology*, 214, 2569–2578. <http://dx.doi.org/10.1242/jeb.057612>
- Mohammed, M., Ootsuka, Y., & Blessing, W. (2014). Brown adipose tissue thermogenesis contributes to emotional hyperthermia in a resident rat suddenly confronted with an intruder rat. *American Journal of Physiology. Regulatory, Integrative and Comparative Physiology*, 306, R394–R400. <http://dx.doi.org/10.1152/ajpregu.00475.2013>
- Myhrvold, C. L., Stone, H. A., & Bou-Zeid, E. (2012). What is the use of elephant hair? *PLOS ONE*, 7, e47018. <http://dx.doi.org/10.1371/journal.pone.0047018>
- Naviaux, J. C., Wang, L., Li, K., Bright, A. T., Alaynick, W. A., Williams, K. R., . . . Naviaux, R. K. (2015). Antipurinergic therapy corrects the autism-like features in the Fragile X (Fmr1 knockout) mouse model. *Molecular Autism*, 6, 1–1. <http://dx.doi.org/10.1186/2040-2392-6-1>
- Nedergaard, J., Alexson, S., & Cannon, B. (1980). Cold adaptation in the rat: Increased brown fat peroxisomal beta-oxidation relative to maximal mitochondrial oxidative capacity. *American Journal of Physiology*, 239, C208–C216.
- Nicolás, L., Martínez-Gómez, M., Hudson, R., & Bautista, A. (2011). Littermate presence enhances motor development, weight gain and competitive ability in newborn and juvenile domestic rabbits. *Developmental Psychobiology*, 53, 37–46. <http://dx.doi.org/10.1002/dev.20485>

- Nobel, P. S. (1978). Surface temperatures of cacti—Influences of environmental and morphological factors. *Ecology*, *59*, 986–995. <http://dx.doi.org/10.2307/1938550>
- Ono, M., Igarashi, T., Ohno, E., & Sasaki, M. (1995). Unusual thermal defence by a honeybee against mass attack by hornets. *Nature*, *377*, 334–336. <http://dx.doi.org/10.1038/377334a0>
- Ophir, A. G., Schrader, S. B., & Gillooly, J. F. (2010). Energetic cost of calling: General constraints and species-specific differences. *Journal of Evolutionary Biology*, *23*, 1564–1569. <http://dx.doi.org/10.1111/j.1420-9101.2010.02005.x>
- Oppenheim, R. W. (1981). Ontogenetic adaptations and retrogressive processes in the development of the nervous system and behaviour: A neuroembryological perspective. In K. J. Connolly & H. F. R. Precht (Eds.), *Maturation and development: Biological and psychological perspectives* (pp. 73–109). Philadelphia, PA: Heinemann Medical.
- Paladino, F. V., O'Connor, M. P., & Spotila, J. R. (1990). Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature*, *344*, 858–860. <http://dx.doi.org/10.1038/344858a0>
- Parmeggiani, P. L. (2003). Thermoregulation and sleep. *Frontiers in Bioscience*, *8*, s557–s567. <http://dx.doi.org/10.2741/1054>
- Pearson, O. P. (1947). The rate of metabolism of some small mammals. *Ecology*, *28*, 127–145. <http://dx.doi.org/10.2307/1930947>
- Pendergrass, M. L., & Thiessen, D. D. (1981). Body temperature and autogrooming in the Mongolian gerbil, *Meriones unguiculatus*. *Behavioral and Neural Biology*, *33*, 524–528. [http://dx.doi.org/10.1016/S0163-1047\(81\)91977-4](http://dx.doi.org/10.1016/S0163-1047(81)91977-4)
- Phillips, P. K., & Heath, J. E. (2001). Heat loss in Dumbo: A theoretical approach. *Journal of Thermal Biology*, *26*, 117–120. [http://dx.doi.org/10.1016/S0306-4565\(00\)00031-0](http://dx.doi.org/10.1016/S0306-4565(00)00031-0)
- Porter, W. P., & Kearney, M. (2009). Size, shape, and the thermal niche of endotherms. *Proceedings of the National Academy of Sciences, USA*, *106*(Suppl. 2), 19666–19672. <http://dx.doi.org/10.1073/pnas.0907321106>
- Prestwich, K. N. (1994). The energetics of acoustic signaling in anurans and insects. *Integrative and Comparative Biology*, *34*, 625–643.
- Prychodko, W. (1958). Effect of aggregation of laboratory mice (*Mus musculus*) on food intake at different temperatures. *Ecology*, *39*, 500–503. <http://dx.doi.org/10.2307/1931760>
- Putz, O., & Crews, D. (2006). Embryonic origin of mate choice in a lizard with temperature-dependent sex determination. *Developmental Psychobiology*, *48*, 29–38. <http://dx.doi.org/10.1002/dev.20109>
- Rango, M., Arighi, A., Bonifati, C., Del Bo, R., Comi, G., & Bresolin, N. (2014). The brain is hypothermic in patients with mitochondrial diseases. *Journal of Cerebral Blood Flow and Metabolism*, *34*, 915–920. <http://dx.doi.org/10.1038/jcbfm.2014.38>
- Rango, M., Arighi, A., & Bresolin, N. (2012). Brain temperature: What do we know? *NeuroReport: For Rapid Communication of Neuroscience Research*, *23*, 483–487. <http://dx.doi.org/10.1097/WNR.0b013e3283534a60>
- Rattenborg, N. C., Mandt, B. H., Obermeyer, W. H., Winsauer, P. J., Huber, R., Wikelski, M., & Benca, R. M. (2004). Migratory sleeplessness in the white-crowned sparrow (*Zonotrichia leucophrys gambelii*). *PLOS Biology*, *2*, e212. <http://dx.doi.org/10.1371/journal.pbio.0020212>
- Retzlaff, E. G. (1939). Studies in mass physiology: Growth rate with the white mouse. *Journal of Experimental Zoology*, *81*, 343–356. <http://dx.doi.org/10.1002/jez.1400810303>
- Richards, S. A. (1970). The biology and comparative physiology of thermal panting. *Biological Reviews of the Cambridge Philosophical Society*, *45*, 223–261. <http://dx.doi.org/10.1111/j.1469-185X.1970.tb01631.x>
- Riedesel, M. L., Cloudsley-Thompson, J. L., & Cloudsley-Thompson, J. A. (1971). Evaporative thermoregulation in turtles. *Physiological Zoology*, *44*, 28–32. <http://dx.doi.org/10.1086/physzool.44.1.30155549>
- Roeder, J. J., & Anderson, J. R. (1991). Urine washing in brown capuchin monkeys (*Cebus apella*): Testing social and nonsocial hypotheses. *American Journal of Primatology*, *24*, 55–60. <http://dx.doi.org/10.1002/ajp.1350240106>
- Rojas, J. M., Castillo, S. B., Folguera, G., Abades, S., & Bozinovic, F. (2014). Coping with daily thermal variability: Behavioural performance of an ectotherm model in a warming world. *PLOS ONE*, *9*, e106897–e106897. <http://dx.doi.org/10.1371/journal.pone.0106897>
- Rook, G. A. W., Lowry, C. A., & Raison, C. L. (2013). Microbial “old friends,” immunoregulation and stress resilience. *Evolution, Medicine, and Public Health*, *2013*, 46–64. <http://dx.doi.org/10.1093/emph/eot004>
- Rozin, P. N., & Mayer, J. (1961). Thermal reinforcement and thermoregulatory behavior in the goldfish, *Carassius auratus*. *Science*, *134*, 942–943. <http://dx.doi.org/10.1126/science.134.3483.942>
- Satinoff, E. (1991). Developmental aspects of behavioral and reflexive thermoregulation. In H. N. Shair,

- G. A. Barr, & M. A. Hofer (Eds.), *Developmental psychobiology: New methods and concepts* (pp. 169–188). Oxford, England: Oxford University Press.
- Satinoff, E. (1996). Behavioral thermoregulation in the cold. *Comprehensive Physiology*, *14*, 481–505. <http://dx.doi.org/10.1002/cphy.cp040121>
- Sato, K. (2014). Body temperature stability achieved by the large body mass of sea turtles. *Journal of Experimental Biology*, *217*, 3607–3614. <http://dx.doi.org/10.1242/jeb.109470>
- Schino, G., & Troisi, A. (1998). Mother–infant conflict over behavioral thermoregulation in Japanese macaques. *Behavioral Ecology and Sociobiology*, *43*, 81–86. <http://dx.doi.org/10.1007/s002650050469>
- Schmidt, M. H. (2014). The energy allocation function of sleep: A unifying theory of sleep, torpor, and continuous wakefulness. *Neuroscience and Biobehavioral Reviews*, *47*, 122–153. <http://dx.doi.org/10.1016/j.neubiorev.2014.08.001>
- Schmidt-Nielsen, K. (1984). *Scaling*. <http://dx.doi.org/10.1017/CBO9781139167826>
- Schneirla, T. C. (1966). Behavioral development and comparative psychology. *Quarterly Review of Biology*, *41*, 283–302. <http://dx.doi.org/10.1086/405056>
- Scribner, S. J., & Wynne-Edwards, K. E. (1994). Thermal constraints on maternal behavior during reproduction in dwarf hamsters (*Phodopus*). *Physiology and Behavior*, *55*, 897–903. [http://dx.doi.org/10.1016/0031-9384\(94\)90077-9](http://dx.doi.org/10.1016/0031-9384(94)90077-9)
- Seebacher, F. (2005). A review of thermoregulation and physiological performance in reptiles: What is the role of phenotypic flexibility? *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology*, *175*, 453–461. <http://dx.doi.org/10.1007/s00360-005-0010-6>
- Seebacher, F., & Grigaltchik, V. S. (2015). Developmental thermal plasticity of prey modifies the impact of predation. *Journal of Experimental Biology*, *218*, 1402–1409. <http://dx.doi.org/10.1242/jeb.116558>
- Seymour, R. S., & Bradford, D. F. (1992). Temperature regulation in the incubation mounds of the Australian Brush-turkey. *Condor*, *94*, 134–150. <http://dx.doi.org/10.2307/1368803>
- Shair, H. N., Masmela, J. R., Brunelli, S. A., & Hofer, M. A. (1997). Potentiation and inhibition of ultrasonic vocalization of rat pups: Regulation by social cues. *Developmental Psychobiology*, *30*, 195–200. [http://dx.doi.org/10.1002/\(SICI\)1098-2302\(199704\)30:3<195::AID-DEV2>3.0.CO;2-K](http://dx.doi.org/10.1002/(SICI)1098-2302(199704)30:3<195::AID-DEV2>3.0.CO;2-K)
- Sheldon, K. S., Yang, S., & Tewksbury, J. J. (2011). Climate change and community disassembly: Impacts of warming on tropical and temperate montane community structure. *Ecology Letters*, *14*, 1191–1200. <http://dx.doi.org/10.1111/j.1461-0248.2011.01689.x>
- Shepherd, B. L., Prange, H. D., & Moczek, A. P. (2008). Some like it hot: Body and weapon size affect thermoregulation in horned beetles. *Journal of Insect Physiology*, *54*, 604–611. <http://dx.doi.org/10.1016/j.jinsphys.2007.12.007>
- Sokoloff, G., & Blumberg, M. S. (1998). Active sleep in cold-exposed infant Norway rats and Syrian golden hamsters: The role of brown adipose tissue thermogenesis. *Behavioral Neuroscience*, *112*, 695–706. <http://dx.doi.org/10.1037/0735-7044.112.3.695>
- Sokoloff, G., & Blumberg, M. S. (2001). Competition and cooperation among huddling infant rats. *Developmental Psychobiology*, *39*, 65–75. <http://dx.doi.org/10.1002/dev.1030>
- Speakman, J. R. (2013). Measuring energy metabolism in the mouse—theoretical, practical, and analytical considerations. *Frontiers in Physiology*, *4*, 34. <http://dx.doi.org/10.3389/fphys.2013.00034>
- Speakman, J. R., & Król, E. (2010). The heat dissipation limit theory and evolution of life histories in endotherms—time to dispose of the disposable soma theory? *Integrative and Comparative Biology*, *50*, 793–807. <http://dx.doi.org/10.1093/icb/icq049>
- Stabentheiner, A., Kovac, H., & Schmaranzer, S. (2002). Honeybee nestmate recognition: The thermal behaviour of guards and their examinees. *Journal of Experimental Biology*, *205*, 2637–2642.
- Stabentheiner, A., Pressl, H., Papst, T., Hrasnigg, N., & Crailsheim, K. (2003). Endothermic heat production in honeybee winter clusters. *Journal of Experimental Biology*, *206*, 353–358. <http://dx.doi.org/10.1242/jeb.00082>
- Steen, I., & Steen, J. B. (1965). Thermoregulatory importance of the beaver's tail. *Comparative Biochemistry and Physiology*, *15*, 267–270. [http://dx.doi.org/10.1016/0010-406X\(65\)90352-X](http://dx.doi.org/10.1016/0010-406X(65)90352-X)
- Stelzner, J. K., & Hausfater, G. (1986). Posture, microclimate, and thermoregulation in yellow baboons. *Primates*, *27*, 449–463. <http://dx.doi.org/10.1007/BF02381890>
- Stern, J. M., & Azzara, A. V. (2002). Thermal control of mother–young contact revisited: Hyperthermic rats nurse normally. *Physiology and Behavior*, *77*, 11–18. [http://dx.doi.org/10.1016/S0031-9384\(02\)00798-9](http://dx.doi.org/10.1016/S0031-9384(02)00798-9)
- Stier, A., Bize, P., Habold, C., Bouillaud, F., Massemin, S., & Criscuolo, F. (2014). Mitochondrial uncoupling prevents cold-induced oxidative stress: A case study using UCP1 knockout mice. *Journal of Experimental Biology*, *217*, 624–630. <http://dx.doi.org/10.1242/jeb.092700>
- Storey, K. B. (2015). Regulation of hypometabolism: Insights into epigenetic controls. *Journal of*

- Experimental Biology*, 218, 150–159. <http://dx.doi.org/10.1242/jeb.106369>
- Stricker, E. M., & Hainsworth, F. R. (1971). Evaporative cooling in the rat: Interaction with heat loss from the tail. *Quarterly Journal of Experimental Physiology and Cognate Medical Sciences*, 56, 231–241. <http://dx.doi.org/10.1113/expphysiol.1971.sp002124>
- Szymusiak, R., & Satinoff, E. (1981). Maximal REM sleep time defines a narrower thermoneutral zone than does minimal metabolic rate. *Physiology and Behavior*, 26, 687–690. [http://dx.doi.org/10.1016/0031-9384\(81\)90145-1](http://dx.doi.org/10.1016/0031-9384(81)90145-1)
- Takahashi, H. (1997). Huddling relationships in night sleeping groups among wild Japanese macaques in Kinkazan Island during winter. *Primates*, 38, 57–68. <http://dx.doi.org/10.1007/BF02385922>
- Tattersall, G. J., Sinclair, B. J., Withers, P. C., Fields, P. A., Seebacher, F., Cooper, C. E., & Maloney, S. K. (2012). Coping with thermal challenges: Physiological adaptations to environmental temperatures. *Comprehensive Physiology*, 2, 2151–2202.
- Terblanche, J. S., Deere, J. A., Clusella-Trullas, S., Janion, C., & Chown, S. L. (2007). Critical thermal limits depend on methodological context. *Proceedings of the Royal Society: Series B, Biological Sciences*, 274, 2935–2943. <http://dx.doi.org/10.1098/rspb.2007.0985>
- Thiessen, D. D. (1983a). Thermal constraints and influences on communication. *Advances in the Study of Behavior*, 13, 147–189. [http://dx.doi.org/10.1016/S0065-3454\(08\)60288-0](http://dx.doi.org/10.1016/S0065-3454(08)60288-0)
- Thiessen, D. D. (1983b). The thermoenergetics of communication and social interactions among Mongolian gerbils. In L. Rosenblum (Ed.), *Symbiosis in parent–offspring interactions* (pp. 113–144). [http://dx.doi.org/10.1007/978-1-4684-4565-7\\_6](http://dx.doi.org/10.1007/978-1-4684-4565-7_6)
- Thompson, D. W. (2014). *On growth and form*. <http://dx.doi.org/10.1017/CBO9781107589070>
- Timberlake, W. D. (2004). Is the operant contingency enough for a science of purposive behavior? *Behavior and Philosophy*, 32, 197–229.
- Tiriac, A., Del Rio-Bermudez, C., & Blumberg, M. S. (2014). Self-generated movements with “unexpected” sensory consequences. *Current Biology*, 24, 2136–2141. <http://dx.doi.org/10.1016/j.cub.2014.07.053>
- Weiss, B., & Laties, V. G. (1961). Behavioral thermoregulation: Behavior is a remarkably sensitive mechanism in the regulation of body temperature. *Science*, 133, 1338–1344. <http://dx.doi.org/10.1126/science.133.3461.1338>
- Whitman, D. W. (1988). Function and evolution of thermoregulation in the desert grasshopper *Taeniopoda eques*. *Journal of Animal Ecology*, 57, 369–383. <http://dx.doi.org/10.2307/4911>
- Wintrode, P. L., & Arnold, F. H. (2001). Temperature adaptation of enzymes: Lessons from laboratory evolution. *Advances in Protein Chemistry*, 55, 161–225. [http://dx.doi.org/10.1016/S0065-3233\(01\)55004-4](http://dx.doi.org/10.1016/S0065-3233(01)55004-4)
- Woods, H. A. (2013). Ontogenetic changes in the body temperature of an insect herbivore. *Functional Ecology*, 27, 1322–1331. <http://dx.doi.org/10.1111/1365-2435.12124>
- Yu, Y., Hill, A. P., & McCormick, D. A. (2012). Warm body temperature facilitates energy efficient cortical action potentials. *PLOS Computational Biology*, 8, e1002456. <http://dx.doi.org/10.1371/journal.pcbi.1002456>