genetic errors in tyrosine/phenylalanine metabolism. Taking advantage of *Aspergillus*' ability to grow using any single amino acid as its sole carbon source, a Spanish research team was able not only to identify the fungal enzyme, but also to use its amino acid sequence as bait in sequence similarity searches against human transcript databases to isolate its human, disease-causing counterpart. Today, there are more than 50 laboratories around the world dedicated to *Aspergillus* research, and in the last decade, small international meetings that are affectionately known as 'Asperfests', have regularly taken place right before major fungal genetics conferences.

Can you tell me something good about **Aspergillus?** Because a great deal of the food eaten by *Aspergillus*, and more generally by fungi, is digested outside of their cells, these organisms possess astounding capabilities in exporting specialized enzymes that break it down, but also for synthesizing and secreting a variety of drugs to protect it from competitors. For example, *Aspergillus niger* is the near exclusive producer of citric acid, a preservative widely used in several different industries as well as a flavor enhancer of a variety of foods and beverages. The ability of *A. niger*, as well as of certain other *Aspergillus* species, to produce a wide variety of products safe for human use and consumption on an industrial scale has earned them the nickname 'cell factories'. Another well known example of an influential *Aspergillus* product is lovastatin, the cholesterol-reducing small molecule that Merck developed into the blockbuster drug Mevacor, which was originally isolated from *Aspergillus terreus*. But the most iconic and tasty *Aspergillus* products are courtesy of *Aspergillus oryzae*, Japan's 'national fungus' — the capacity of this organism to turn starch-rich grains, like rice and soy beans, into sugars makes it essential in the making of several different traditional Far-Eastern drinks and sauces, like the rice wine sake and soy sauce.

How about something bad?
Aspergillus' penchant for making drugs, including disease-preventing ones, means that it can also produce some very potent toxins. Aflatoxin, a potent carcinogen and the causative agent of the mysterious Turkey X disease that killed tens of thousands of birds in England in the early 1960s,

is the most notorious one. Produced by *Aspergillus flavus*, aflatoxin frequently finds its way into human food and animal feeds thanks to the organism's ability to infect several major crops — to this day, consumption of aflatoxin-laced food around the globe results in a handful of human deaths per year as well as in billions of dollars in crop yield losses. In addition to *A. flavus*, several other *Aspergillus* species are opportunistic pathogens to a remarkably wide diversity of hosts. For example, *A. fumigatus* is the leading cause of human aspergillosis, a wide spectrum of diseases that results following inhalation of their highly abundant spores in individuals with compromised immune systems, and is one of the most common and deadly fungal opportunistic pathogens. *A. fumigatus* was also detected in many of the mold-contaminated steroid injections in the recent fungal meningitis epidemic that killed more than 3 dozen humans across the US. In contrast, in the 1990s an outbreak of infections caused by *Aspergillus sydowii* on sea fan corals resulted in dramatic coral die-offs, threatening the collapse of the entire ecosystem of gorgonian coral communities in the Caribbean. As biotic (*e.g.*, the emergence of HIV altered the human disease landscape, dramatically increasing fungal infections) and abiotic (*e.g.*, changes in climate are a major factor in emerging fungal-driven plant diseases) factors continue to shape the relationships between microbes and potential hosts, *Aspergillus*' proclivity toward opportunistic pathogenesis is something to watch out for.

Where can I find out more?
Gibbons, J.G., and Rokas, A. (2013). The function and evolution of the *Aspergillus* genome. Trends Microbiol. *21*, 14–22.
Latge, J.-P., and Steinbach, W.J. (2008). *Aspergillus fumigatus* and Aspergillosis (ASM Press, Washington, DC).
Osmani, A., and Goldman, G.H. (2008). The Aspergilli: Genomics, Medical Aspects, Biotechnology, and Research Methods (CRC Press, Boca Raton, FL).
Penalva, M.A. (2001). A fungal perspective on human inborn errors of metabolism: alkaptonuria and beyond. Fungal Genet. Biol. *34*, 1–10.
Samson, R.A., and Varga, J. (2007). *Aspergillus* Systematics in the Genomics Era. Stud. Mycol., volume *59*.
Scazzocchio, C. (2009). *Aspergillus*: a multifaceted genus. In Encyclopedia of Microbiology (3rd edition), M. Schaechter, (Boston, MA: Academic Press), pp. 401–421.

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Hibernation

Fritz Geiser

Hibernation (multiday torpor) and daily torpor in heterothermic mammals and birds are characterized by pronounced temporal reductions in body temperature, energy expenditure, water loss, and other physiological functions and are the most effective means for energy conservation available to endotherms. Hibernators express multiday torpor predominately throughout winter, which substantially enhances winter survival. In contrast, daily heterotherms use daily torpor lasting for several hours during the rest phase. Although torpor is still widely considered to be a specific adaptation of cold-climate species, as we will see in this primer, it is used by many diverse species from all climate zones, including the tropics. While energy conservation during adverse conditions is an important function of torpor, it is also employed to permit energy-demanding processes such as reproduction and growth, especially when food supply is limited. Even migrating birds enter torpor to conserve energy for the next stage of migration. Although many heterothermic species will be challenged by anthropogenic influences such as habitat destruction, introduced species, novel pathogens and specifically global warming, not all are likely to be affected in the same way. In fact, as argued here, it is likely that opportunistic heterotherms may be better equipped to deal with these challenges than homeotherms because heterotherms have highly flexible energy requirements, can limit foraging and reduce the risk of predation, and often are also long-lived. In contrast, strongly seasonal hibernators, especially those restricted to mountain tops, and those that have to deal with new diseases that are difficult to combat at low body temperatures, are likely to be adversely affected.

A cool advantage
Living organisms are either ectothermic or endothermic.
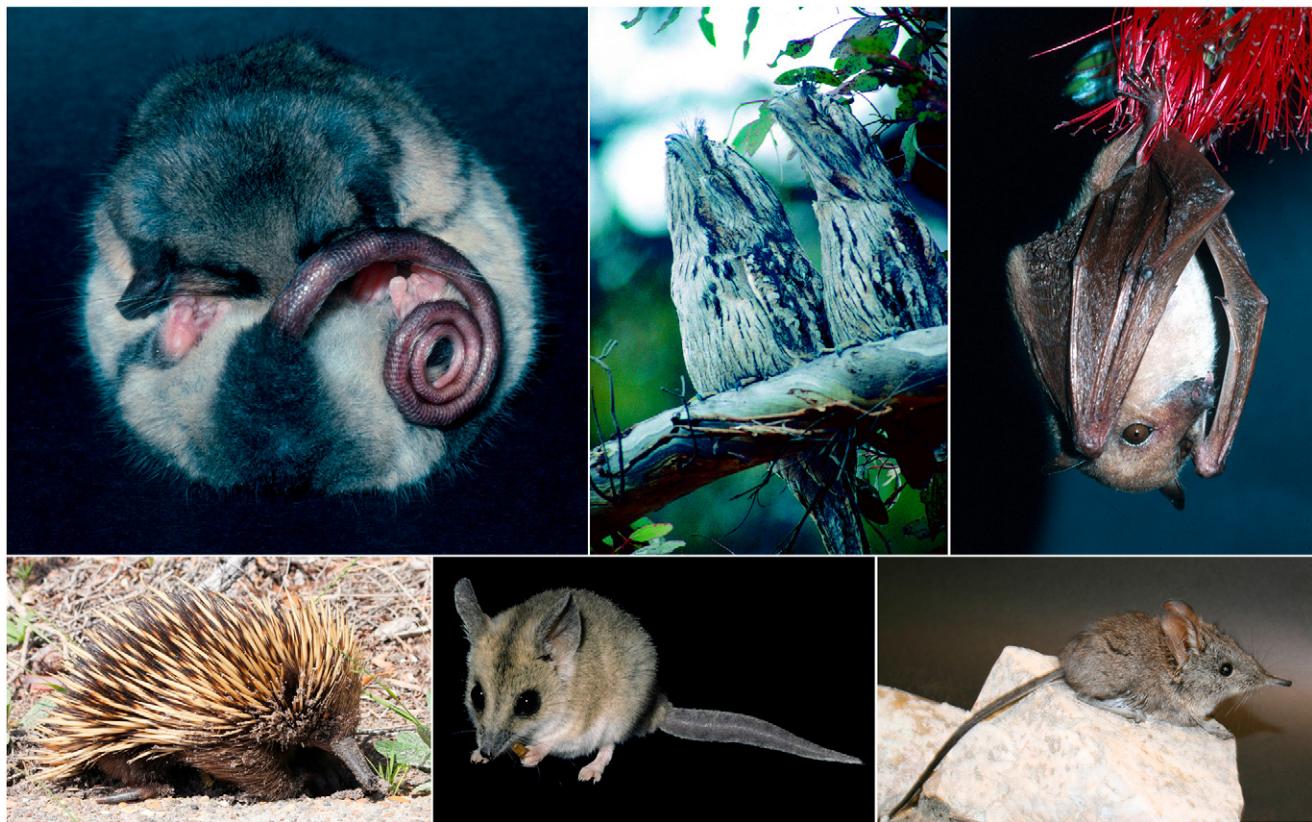
Figure 1. Heterothermy in the animal world.
Depicted is a sample of heterothermic species. The endangered mountain pygmy-possum (*Burramys parvus*, 50 g; top-left) is restricted to high mountain peaks of the Australian alps where it hibernates under snow-covered boulder fields for ~5–6 months. The possum adopts the typical ball-shape of many torpid hibernators, but it has been turned on its back to show head and appendages. The tawny frogmouth (*Podargus strigoides*, 500 g; top-middle) is found all over the Australian continent, enters daily torpor at night and/or in the early morning, and is the largest bird known to use torpor. The nectarivorous northern blossom-bat (*Macroglossus minimus*, 16 g; top-right) is distributed over tropical Australia and south-east Asia. It is one of the smallest megabats and enters daily torpor. The short-beaked echidna (*Tachyglossus aculeatus*, ~3 kg; bottom-left), an egg-laying mammal, is distributed over the entire Australian continent and hibernates in many areas.The fat-tailed dunnart (*Sminthopsis crassicaudata*, 15 g; bottom-middle), a dasyurid marsupial, is found in arid and semi-arid areas in the southern half of Australia and uses daily torpor throughout winter. The Cape rock elephant-shrew (*Elephantulus edwardii*, 45 g; bottom-right) is restricted to medium high elevations of South Africa and displays short-term hibernation. See Table 1 for a more comprehensive list of heterothermic species.

Ectotherms have low metabolic rates, lack insulation and therefore their body temperature (T_b) is a function of ambient temperature (T_a). The vast majority of plants and animals are ectothermic and, because they do not 'waste' energy on internal heat production for thermoregulation, their energy and nutrient requirements are low, but they and their bodily functions are directly affected by the temperature of their environment.

Endotherms, on the other hand, have metabolic rates that are many-fold higher than those of ectotherms and therefore their energy requirements are high. Endotherms usually insulate their bodies to minimize heat loss. This permits 'homeothermic' thermoregulation with maintenance of T_b between

~32 and ~42°C at a rather constant level over a wide range of T_a, largely by adjustments of internal heat production that is proportional to heat loss. Endotherms include most mammals and birds, but some fishes, reptiles, insects, and flowers are also fully or partially endothermic. While a constant high T_b optimizes the function of the organism, it comes at a high energetic cost. This is especially critical for mammals and birds because the vast majority of species are small and heat loss increases with decreasing size as a result of increasing relative surface area. Small size also limits the relative amounts of fat that can be stored and the thickness of insulation that can be carried. As heat loss is a function of the T_b-T_a differential, thermoregulatory costs at low T_a may

become prohibitively high in small endotherms, especially when energy availability is low.

To deal with energetic and other challenges, not all endotherms are permanently homeothermic (i.e., have a constant high T_b); rather, many are 'heterothermic' (i.e., core T_b shows temporal changes) and, during certain times of the day or year, enter a state of torpor (see Figure 1 for examples). Mammalian and avian torpor (including hibernation and daily torpor) is characterized by temporal, substantial but controlled reductions in T_b, metabolic rates, water loss, heart rate and other physiological functions and is the most effective means for energy conservation available to endotherms. Torpor conserves energy because thermoregulation at
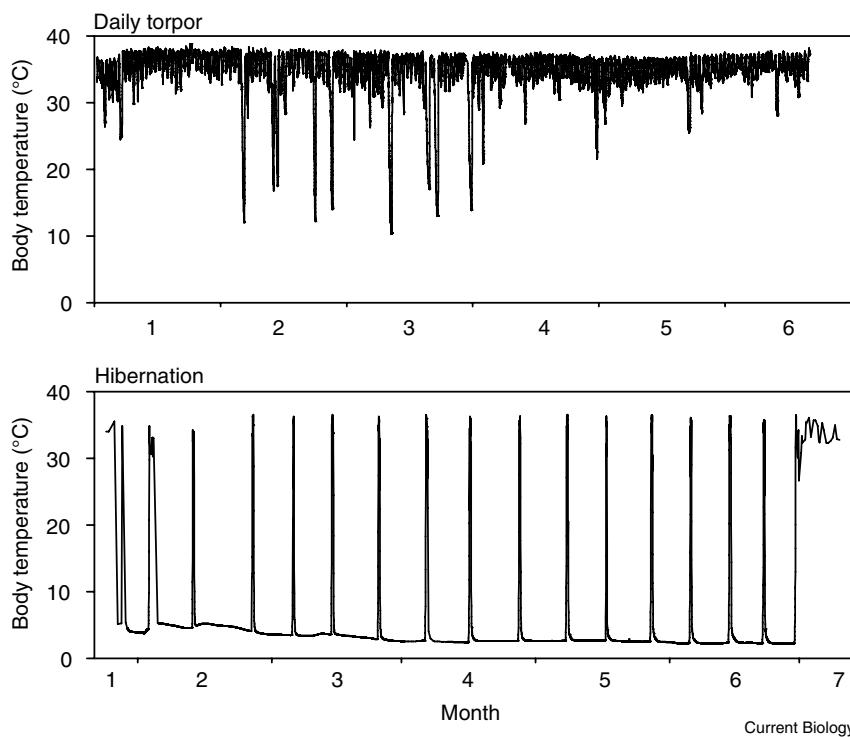
Figure 2. Patterns of daily torpor and hibernation.
Patterns of daily torpor and hibernation in free-ranging mammals over several months in the cold season (autumn months, 1–2; winter months, 3–5; and spring months, 6–7). The species are sugar gliders (*Petaurus breviceps*) for daily torpor and mountain pygmy-possums (*Burramys parvus*) for hibernation. Body temperatures were measured using temperature telemetry.

high T_b is abandoned, the T_b falls and inhibits metabolism, and because some species can use metabolic inhibition to further enhance energy savings. Although the reduction of metabolism and T_b during torpor in heterothermic endotherms and ectotherms may appear similar, heterotherms, unlike ectotherms, can rewarm from the low T_b during torpor by using internal heat production. Further, although torpid endotherms thermo-conform over a wide range of T_b, low T_bs during torpor (often between 0 and 20°C) are regulated at or above a species-specific minimum by an increase in heat production to prevent tissue damage at low T_b and to maintain the ability of active rewarming from torpor — most ectotherms simply freeze to death.

Torpor in most heterothermic species occurs either on a daily basis ('daily torpor' in the 'daily heterotherms') or on a seasonal basis in the 'hibernators' (Figure 2). Daily heterotherms remain torpid for only part of the day, but usually continue to forage during their active 'normothermic' phase (i.e., when T_b is regulated at constant, high levels).

In contrast, the state of torpor in hibernating species may last for several days or weeks in winter and many remain in their hibernacula throughout this time.

Heterothermy: function and diversity

Hibernation often is strongly seasonal and lasts from late summer/autumn to late winter/spring, and, in the past, was viewed mainly as an adaptation to the cold. As hibernation is now known to occur in many habitats from the arctic to the tropics it appears that lack of food, which occurs for part of the year in dry tropical areas as well as in cold temperate and arctic areas, is the main reason for its use. Obviously, because low T_as require an increase in thermoregulatory energy expenditure in normothermic individuals and cold often is a reason for low food availability, cold exposure generally enhances the use of torpor.

Currently, known hibernators include many mammals from all three mammalian subclasses (Monotremes, Marsupials, Placentals), but only

a single bird species, the poorwill (Table 1). Hibernators that express deep torpor with a substantial reduction of T_b usually from ~37°C to ~5°C, with a minimum of –3°C, are small and weigh between ~5 g and ~5 kg. However, large carnivores, such as black bears (*Ursus americanus*), also exhibit a form of hibernation at relatively high T_b of ~30°C. Many hibernators fatten extensively before the hibernation season, do not hibernate when lean, and rely to a large extent on stored fat as an energy source in winter; some species use food caches or a combination of fat and caches.

Although torpor in many hibernators is expressed throughout the 'hibernation season' in winter, most do not remain continuously torpid (Figure 2). Bouts of multiday torpor, during which T_b is low and bodily functions are reduced to a minimum, are interrupted by periodic, energetically costly rewarming and brief (usually <1 day) normothermic resting periods that together use up most of the energy required during hibernation. Importantly, the duration of torpor bouts in hibernators is strongly temperature-dependent and, although torpor bouts may last for up to a month at low T_a/T_b, at high T_a of ~20 to 25°C they often are <24 hours and superficially appear to be daily torpor.

While hibernation with periodic arousals in winter followed by activity and reproduction in spring/summer is a widely employed pattern, this is not universal. Some species such as marsupial pygmy-possums (*Cercartetus* spp.) or insectivorous bats are rather flexible with their torpor/activity patterns and, especially those that live in milder areas, may forage during warm spells in winter and then re-enter multiday torpor when the weather turns cold. In non-reproductive dormice (*Glis glis*), hibernation may be terminated in late spring, but individuals may re-enter a period of multiday summer torpor (estivation) after only a few days of activity. In contrast, in reproductive echidnas (*Tachyglossus aculeatus*) hibernation is often terminated in mid-winter for mating (Figure 1 and Table 1). Recent evidence also shows that not all hibernators rewarm periodically. Tenrecs (*Tenrec ecaudatus*) may remain at low T_b

Table 1. Heterothermic birds and mammals.

Birds
Songbirds (Passeriformes): Nocturnal shallow torpor in a number of species.
Kingfishers (Coraciiformes): Todies and Kookaburras enter shallow daily torpor.
Mouse birds (Coliiformes): Daily torpor in several species.
Swifts (Apodiformes): Several swifts enter nocturnal torpor.
Hummingbirds (Trochiliformes): Many hummingbirds enter torpor at night.
Nightjars (Caprimulgiformes): Torpor is used by many nightjars including poorwills (*Phalaenoptilus nuttallii*), the only avian species known to hibernate, and the tawny frogmouth (*Podargus strigoides*), the largest bird know to use torpor.
Owls (Strigiformes): Shallow torpor in Scops owls.
Pigeons (Columbiformes): Several species enter torpor at night.

Mammals
Egg-laying mammals (Monotremata): Echidnas hibernate in many areas of Australia.
Opossums (Didelphimorpha): Several small south American opossums enter daily torpor.
Shrew-opossum (Microbiotheria): The Monito del monte hibernates in southern Chile.
Carnivorous marsupials (Dasyuromorphia): Many dasyurids <1 kg enter daily torpor.
Marsupial moles (Notoryctemorphia): Marsupial moles are heterothermic.
Possums (Diprotodontia): Pygmy-possums and feathertail gliders hibernate; other gliding possums use daily torpor.
Tenrecs, golden moles (Afrosoricida): Tenrecs hibernate or express torpor; golden moles are heterothermic.
Elephant shrews (Macroscelidea): Short-term hibernation and daily torpor.
Armadillos (Edentata, Cingulara): Hibernation in at least one species of armadillo.
Rodents (Rodentia): Hibernation and daily torpor are widespread among rodents.
Primates (Primates): Hibernation in fat-tailed lemurs and other small lemurs, daily torpor in bushbabies.
Insectivores (Insectivora, Lipotyphla): Hedgehogs hibernate; shrews use daily torpor.
Bats (Chiroptera): Hibernation in many insectivorous bats; small fruit bats use daily torpor.
Carnivores (Carnivora): Shallow hibernation in bears and badgers; shallow torpor in skunk.

of ~23°C for >4 months, similar to hibernation in ectotherms, whereas fat-tailed lemurs (*Cheirogaleus medius*) and related species undergo cycles of T_b that fluctuate largely passively with T_a for months, but T_b remains below normothermic levels. Passive or partially passive rewarming, which reduces the energetic costs of rewarming from torpor enormously, is also widely used by bats and poorwills, but this is, of course, only possible if the T_a fluctuates within the T_b range of the animal, which will not occur in cold climates, or if animals have access to solar radiation.

Hibernators are extremely efficient in reducing their metabolic rates during torpor (TMR), even under relatively warm conditions. On average, TMR is reduced to ~5% of the basal metabolic rate (BMR, often considered to be the minimum metabolic rate in endotherms), but can be <1% of that in normothermic individuals, especially at low T_a. Even when the high cost of periodic arousals is considered, energy expenditure during the entire mammalian hibernation season is still reduced to <15% and may be as little as 4% of that of an animal remaining normothermic throughout winter. This enormous reduction in energy expenditure is perhaps best illustrated by the fact that many hibernating mammals can survive

entirely on body fat gained during pre-hibernation fattening, often for six months and up to one year.

Daily heterotherms, unlike hibernators, always express daily torpor independent of T_a, season and trophic state. Daily torpor lasts only for hours rather than days or weeks (Figure 2), is usually not as deep as hibernation, and is often interrupted by activity and feeding. It is likely because of this fact that daily torpor was only discovered in the sixties, when scientists at UCLA noticed that their sluggish mice were not sick but rather torpid, whereas hibernation has been known for centuries. Daily torpor often occurs during the inactive phase: nocturnal species enter torpor late at night or in the early morning, whereas diurnal species enter torpor early in the night. Daily torpor is generally less seasonal than hibernation, and can occur throughout the year, although its use often increases in winter. In some warm climate species, however, daily torpor is more pronounced in summer than in winter and this unusual seasonal pattern appears to be due to reduced food or water availability in summer. In desert dwelling species that have adapted to a generally low availability of food, daily torpor appears to be used regularly to balance daily energy budgets even when environmental conditions

appear favourable, rather than in response to acute energy shortages.

Many daily heterotherms, unlike hibernators, do not show extensive fattening before winter, most weigh between 3 g and 1 kg and enter torpor only when lean. The T_bs in typical daily heterotherms, such as small carnivorous marsupials and mice, usually fall from ~37°C to ~15°C, although in some hummingbirds T_bs below 10°C have been reported, whereas in large species T_b is maintained just below 30°C. The TMR during daily torpor is on average reduced to ~30% of the BMR, although this percentage is strongly affected by body mass and other factors. Overall, daily energy expenditure is usually reduced by 10–80% on torpor days in comparison to days when animals remain normothermic, primarily depending on the duration of the torpor bout and torpor depth.

Beyond winter survival
Energy conservation during winter torpor clearly is an important adaptation as it permits survival on limited food at low T_a. However, energetic bottlenecks can also be caused by high energy demands such as during reproduction, development or migration because extra energy must be obtained to fuel activity and growth in addition to thermoregulatory costs. Torpor

has the potential of mitigating these demands and is used accordingly.

Many endotherms reproduce when food is abundant and appear to avoid torpor to expedite the production of offspring. Others must reproduce with limited or fluctuating resources and some of these animals use torpor during reproduction. Torpor during pregnancy has been observed in echidnas, several small marsupials, tenrecs, mouse lemurs, several insectivorous bats and blossom-bats. Whereas torpor during pregnancy appears to be used mainly during energetic stress, some species use it to enhance fat storage. The marsupial mulgara (*Dasycercus cristicauda/blythi*) enters spontaneous torpor (food available) under thermally mild conditions during pregnancy and fattens during this time. Thus, in this case, it appears that torpor is not a response to acute energy shortage or thermal stress, but rather a predictive response to reduce energy loss and enhance fat storage for lactation, which is the energetically most demanding time of reproduction in marsupials. In pregnant hoary bats (*Lasiurus cinereus*), torpor during cold spells in spring appears to be used for energy conservation, but also to slow embryonic growth to delay parturition until conditions are more favourable for neonatal survival and lactation. However, torpor even occurs during lactation in small marsupials, some bats and mouse lemurs. While low T_b during lactation will slow milk production and the development of young, it will enhance the chance of survival of young during adverse conditions.

Most endotherms are altricial (i.e., small, undeveloped and naked) at hatching/birth. Their growth and development is achieved on imported nutrients usually supplied by their parents. The largely thermo-conforming response by these young early during development permits the use of nutrients mainly for growth. However, when the developing young begin to use energy for endothermic thermoregulation at ~30 to 50% of adult size, they face the problem of excessive heat loss. To minimize energy loss when parents are unable to supply enough food, some growing young use torpor. Torpor during development occurs in several birds and mammals and appears to

have two major functions: survival of adverse conditions, as in many adult heterotherms, and enhancement of growth when food is limited.

By autumn, most young have grown to near adult size and, in strongly seasonal climates, must decide whether to stay and face the winter, or go. Birds can fly and therefore migrate and avoid winters. However, migration is energetically demanding and food supply en route may be unpredictable. It appears that for these reasons migrating hummingbirds, even when relatively fat, employ torpor to enhance energy storage at night for the next stage of migration. Therefore, torpor use in migrating hummingbirds and perhaps other birds, similar to pregnant mulgaras, is a predictive response that anticipates likely energetic bottlenecks in the future.

The new challenges
Heterothermic mammals and birds, like other organisms, are subject to anthropogenic influences, including habitat destruction, introduction of predators or competitors, exposure to new pathogens and climate change. Some of these may appear especially challenging to heterotherms, which are supposed to be immobile at low T_b and vulnerable to predators, and require low T_a for torpor expression. While this is correct in some cases, the situation is complex and some heterothermic species may actually do better than one might expect.

Inactivity and immobility during torpor and thus increased risk of predation are widely viewed as one of the major risks associated with torpor and that its use would therefore be minimized whenever possible. However, torpid mammals are not entirely immobile and movement during torpor at T_b as low as 15°C permits both basking during passive rewarming to enhance energy savings, and predator avoidance. Moreover, torpor is not always avoided whenever energetically possible. Summer torpor in dormice (*Glis glis*) in good condition and with access to food, and in fat subtropical bats (*Nyctophilus bifax*), suggests that these species use torpor not because of food shortages and low energy stores, but to minimize foraging and thus avoid predation when feeding is not required.

Reduced predation appears be an important reason why heterothermic mammals are less threatened by extinctions and have suffered far less extinctions than their homeothermic relatives. But perhaps even more importantly, opportunistic heterotherms can minimize the risk of extinction because of their often large geographic ranges and enormous scope for adjusting energy requirements. This may allow long-term survival of adverse environmental conditions and help deal with habitat degradation in addition to avoidance of predators. Thus, the use of torpor and the often prolonged life span, which permits survival of extended adverse conditions and increases potential reproductive output, appear to have permitted opportunistically heterothermic mammals to cope with anthropogenic disturbances better than is the case in many homeotherms.

However, some heterotherms are directly threatened by global warming and introduction of foreign pathogens. Many hibernating mammals are restricted to mountain tops that do not permit further altitudinal adjustments with climate change and often persist because hibernation permits them to deal with severe winters that cannot be endured by others. Warming will result in increased competition and predation because homeothermic species now can invade. Moreover, in many of these high altitude mammals the period of winter dormancy will be disrupted by a change in the seasonality of weather. Other risks associated with hibernation at low T_b are suppression of immunological responses. One specific example is the white nose syndrome that is devastating populations of hibernating bats in North America. It is likely that new foreign pathogens will affect other hibernating organisms in the future.

Perspectives
Hibernation and daily torpor are used for energy conservation in many diverse mammals and birds from all climate zones. However, torpor is not only used to deal with acute energetic challenges, but also to permit reproduction and growth on a limited or fluctuating food supply. Much of the new understanding

about the diversity and functions of torpor has been gained from work on free-ranging animals in the wild or using a comparative approach on many species from diverse habitats. Less progress has been made on understanding the mechanisms of the enormous functional differences between homeothermic and heterothermic species. For example, the reasons for the much higher thermal and ischemic tolerance of tissues of hibernators than those of homeotherms are still not understood, although these may have spin-offs for organ storage and other aspects of human medicine. Some potential applications include cardiac surgery or other organ transplants that have to be conducted at relatively high temperatures to avoid tissue damage, but could be better performed at low temperatures. Further, an understanding of the reasons behind the low muscle disuse atrophy in hibernators, despite extremely long inactive phases, has obvious implications for long-term hospital care.

Further reading

Barnes, B.M., and Carey, H.V. eds. (2004). Life in the Cold: Evolution, Mechanisms, Adaptation, and Application. 12th International Hibernation Symposium. Biological Papers of the University of Alaska #27. (Fairbanks: University of Alaska).

Geiser, F. (2004). Metabolic rate and body temperature reduction during hibernation and daily torpor. Annu. Rev. Physiol. 66, 239–274.

Geiser, F., and Brigham, R.M. (2012). The other functions of torpor. In Living in a Seasonal World. T. Ruf, C. Bieber, W. Arnold, E. Millesi, eds. (Heidelberg: Springer Verlag), pp. 109–121.

Lane, J.E., Kruuk, L.E.B., Charmantier, A., Murie J.O., and Dobson F.S. (2012). Delayed phenology and reduced fitness associated with climate change in a wild hibernator. Nature 489, 554–557.

Lovegrove, B.G., and McKechnie, A.E. eds. (2008). Hypometabolism in animals: torpor, hibernation and cryobiology. 13th International Hibernation Symposium. (Pietermaritzburg: University of KwaZulu-Natal).

Lyman, C.P., Willis, J.S., Malan, A., and Wang, L.C.H. (1982). Hibernation and Torpor in Mammals and Birds (New York: Academic Press).

Rojas, A.D., Körtner, G., and Geiser, F. (2012). Cool running: locomotor performance at low body temperature in mammals. Biol. Lett. 8, 868–870.

Ruf, T., Bieber, C. Arnold, W., and Millesi, E. eds. (2012). Living in a Seasonal World. (Heidelberg: Springer Verlag).

Tattersall, G.J., Sinclair, B.J., Withers, P.C., Field, P.A., Seebacher, F., Cooper, C.E., and Maloney, S.K. (2012). Coping with thermal challenges: physiological adaptations to environmental temperature. Compr. Physiol. 2, 2151–2202.

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Spatiotopic neural representations develop slowly across saccades

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One of the long-standing unsolved mysteries of visual neuroscience is how the world remains apparently stable in the face of continuous movements of eyes, head and body. Many factors seem to contribute to this stability, including rapid updating mechanisms that temporarily remap the visual input to compensate for the impending saccade [1]. However, there is also a growing body of evidence pointing to more long-lasting spatiotopic neural representations, which remain solid in external rather than retinal coordinates [2–6]. In this study, we show that these spatiotopic representations take hundreds of milliseconds to build up robustly.

Aftereffects have proven to be an effective tool to study spatiotopy, as an eye movement between adaptation and test dissociates retinal from external space. We use the tilt aftereffect, previously shown to have a spatiotopic component [2] (but not without controversy [7]). Twelve subjects (11 naïve to the goals of the study) adapted to a tilted (±15°) grating patch, then saccaded on cue to a target 20° to the right. A similar-sized test grating of variable tilt then appeared at either the same screen or retinal position as the adapter, or an unmatched position (Figure 1A). Subjects reported whether it appeared to be tilted clockwise or counter-clockwise, and the proportion of clockwise responses fit with a Gaussian error function to calculate the tilt necessary to annul the illusion (see Figure S1 in the Supplemental Information). The magnitude of the aftereffect was defined as half the difference of tilt to annul the effects of adapting to clockwise compared with counter-clockwise gratings. Data were also collected without eye movements in a matched spatial location ('full adaptation') to give a baseline measure of the effect.

The key manipulation of this study was to display the saccadic target for a variable duration before cueing subjects to saccade (by the extinction of the fixation point; Figure 1A). Figure 1B shows the average strength of the tilt aftereffect, as a function of preview duration. Previewing the target before initiating the saccade reduced slightly the strength of both full adaptation and retinotopic adaptation, presumably because the aftereffect decreased with duration after adaptation (bootstrap sign test between 0 and 1000 ms: p = 0.03). However, target preview had the opposite effect in the spatiotopic condition, where adaptation increased with preview duration to reach the strength of retinotopic adaptation at 1000 ms. (bootstrap sign test between 0 and 1000 ms: p < 0.001; see Figure S1B in the Supplemental Information for individual results). Figure 1C illustrates this more clearly, plotting retinotopic and spatiotopic adaptation as a proportion of full-adaption strength. Whereas retinotopic adaptation remains quite constant, spatiotopic adaptation builds up over time, from 16% for the reactive saccades (similar to the control condition), to 67% of the full adaptation effect at 1000 ms. Bootstrap sign tests show that the spatial aftereffect is significantly different from the aspecific effect at 500 ms (p < 0.001) and 1000 ms (p < 0.001), but not at 0 ms (p = 0.12).

To be certain that subjects complied with instructions, eye movements were monitored on every trial, and trials discarded if the eyes did not arrive within 4° of target, or were not stationary on probe onset. This ensured that there was no spillage of retinotopic adaptation to the spatiotopic condition, and that in all cases the test overlapped with at least 50% of the adaptor grating. Supplemental Figure S2 plots the scatter of eye positions at the time of probe presentation for the various conditions, showing that there were no systematic biases that could explain the results. There was also no systematic variation in probe presentation time relative to saccade offset, or other aspects of the saccade dynamics were observed that could account for the differences (see Table in Supplemental Figure S2).

The results provide clear evidence for the existence of a spatiotopic representation of orientation, one that can be distorted by adaptation,