

Food, Energy, and Temperature *at Work:* The Lives of Mammals in Frigid Places

Reindeer (*Rangifer tarandus*), which occur in Siberia and other far-northern regions, typically give birth in May, when the ground remains snow-covered and the air often cools to below 0°C overnight. At the moment of its birth, a reindeer calf experiences a drop in its environmental temperature from 37°C inside its mother's uterus to the prevailing air temperature. If the air temperature is -3°C, the calf's environmental temperature plummets by 40°C at birth. The air sometimes is much colder, and some calves experience a drop of 50–60°C when they are born. Newborns are wet—covered with amniotic fluid—and a strong wind may blow.

Reindeer calves must thermoregulate on their own from the moment they are born, or die, because they do not huddle with each other or with adults, and they have no nest to protect them. They are perhaps the most precocial (adultlike) of all the newborns of land mammals. They stand the moment they are born. When 2 days old, they can run faster than a person. Because herds typically move from place to place incessantly to find food, the newborn calf has no luxury of resting to gather strength. It must keep up. Within a week, a reindeer calf can swim across broad rivers.

As stressed in Chapter 4, the physiology of young animals is as important as the physiology of adults, because each individual animal must survive first as a youngster if it is ever to have the chance of surviving (and reproducing) as an adult. We will return to the young of reindeer shortly. First, however, let's focus on adult reindeer and the environment in which they live—matters that set the context for fully understanding the young.

Food, Nutrition, Energy Metabolism, and Thermoregulation in the Lives of Adult Reindeer

Reindeer, as a species, are probably the most adapted of all inland mammals to cold exposure; some herds live year-round in places where the average annual temperature is below -5°C. An intriguing aspect of animal species that are extremely well suited physiologically to live in stressful habitats is that their very presence can permit *other* species to exist there as well. In deserts, the existence of rodents that have evolved extremely low requirements for ingested water permits many water-dependent predators to exist as well; the rodents provide the watery food the predators need. Similarly, in the Far North, the existence of reindeer permits the existence there of wolves and other predators—including indigenous human cultures. During preindustrial times, people could not possibly have survived in the interior of the Far North on their own. The existence of humankind there was made possible, all around the Arctic, by herds of reindeer, which served as sources of food and of highly insulating pelts that people employed for necessary shelter and clothing. The same points still apply today to a number of indigenous human cultures that live apart from modern comforts, such as some communities of Sami people in Scandinavia.

A newborn reindeer calf must thermoregulate on its own

Although mother reindeer feed their young, they do not keep them warm, and the Arctic environment where birth occurs may be very cold.



Because of the intimate relations between reindeer and people over long periods in the past, reindeer were domesticated to some degree in many regions. Today, therefore, the species consists of both wild populations and numerous domesticated strains or races. Caribou are considered by most mammalogists to be the same species. As adults, reindeer in some populations are roughly the same size as humans.¹

Reindeer have many characteristics that help them prosper in the Far North. Although adult reindeer weigh, on average, about one-third as much as adult moose (another northern species), the feet of reindeer are so unusually broad that the contact area of a reindeer with the ground is about the same as that of a moose. Accordingly, the downward gravitational force on each unit of area of a reindeer's feet is very low compared with that of a moose, explaining how reindeer can readily negotiate snow fields that stop moose.

Adult reindeer in their winter pelage have lower-critical temperatures of -30°C or lower in still air. The air temperature in the Arctic rarely goes below -50°C . Thus the air temperature does not drop far below their lower-critical temperature, and reindeer in their winter pelage in still air never have to increase their metabolic rates by much above basal (Figure 11.1). As an amusing comparison, Laplanders and Norwegians equipped just with the insulation "nature gave them" (i.e., naked) have lower-critical temperatures of $+24$ – 27°C ! Only by dressing in something like a reindeer pelt can a person have a lower-critical temperature that is compatible with Arctic life.

One reason for the low energy costs of adult reindeer in the frigid air of winter is their pelage. A dense underfur of fine hairs thickly covers their skin, and the longer "guard" hairs of the pelage, which protrude beyond the underfur and hang over its outer surface, are extensively vacuolated ("hollow"). In common with other large species of mammals, reindeer undergo dramatic seasonal molts. In winter, a reindeer's fur is 3–4 cm thick over much of its body

¹Various subspecies and herds of reindeer differ in average adult weight. In some, the average adult weight is 60–70 kg, the same as the nominal average adult weight of people. In others, the average is twice as great, or even, in some cases, three times as great.

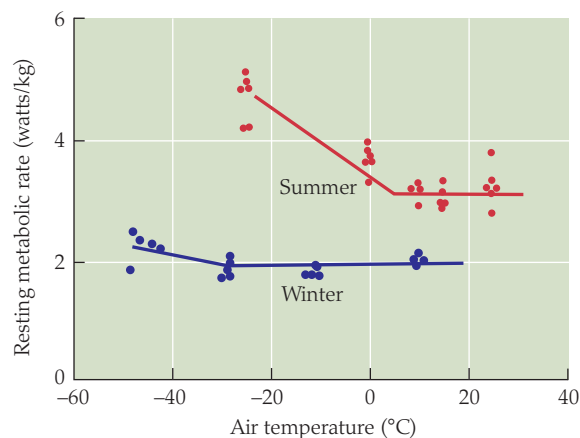


FIGURE 11.1 Resting metabolic rate as a function of air temperature down to -50°C in adult reindeer The same Norwegian animals, weighing about 70 kg, were studied in winter and summer. The air was still. Lines are drawn by eye to approximate the trends in the data. (After Nilssen et al. 1984.)

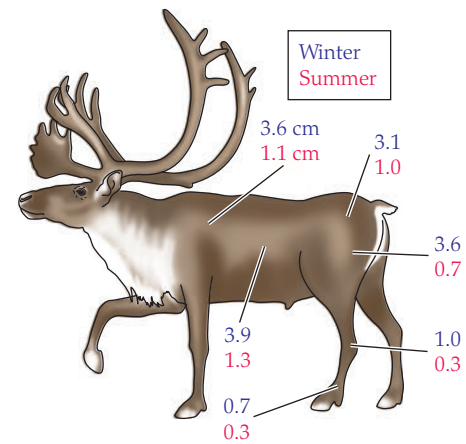


FIGURE 11.2 Fur thickness of adult reindeer in winter and summer The thickness was measured perpendicular to the skin surface and is expressed in centimeters. (After Johnsen et al. 1985.)

(Figure 11.2). All body surfaces of a reindeer, even the nose, have a hair covering.

Besides the pelage, another reason for the low energy costs of adult reindeer in frigid air is that they employ regional heterothermy. Reindeer do not keep the tissues of their legs and other exposed body parts as warm as their body core (see Figure 10.32).

Reflecting on what we learned about lipid fluidity in our study of fish and other poikilotherms in Chapter 10, an interesting question about the heterothermic legs of reindeer is whether the lipids in their legs are hard and stiff where the limbs are cold, much as butter is hard when cold. Actually, it is a matter of ancient knowledge that lipids from the outer extremities of reindeer legs—and also those from the hooves of cattle—are particularly fluid, compared with body-core lipids. People have long used lipids (oils) from the outer extremities to soften boot leather and give flexibility to leather bow strings in cold climates.

Homeoviscous adaptation exists from one end of a heterothermic leg to the other: Whereas the lipids in the upper leg of a reindeer or cow have chemical structures that give them a gel-like texture at 37°C and cause them to become hard at 0°C , the lipids from the outer extremities have different chemical structures that give them a gel-like or oily texture near 0°C . One way to examine the spatial diversity of chemical structure is to look at the abundances of key, diagnostic fatty acids in the marrow lipids of the limb bones. As seen in Figure 11.3, oleic acid—an unsaturated fatty acid—becomes a dramatically more abundant constituent of the marrow lipids as one moves out along a leg, whereas palmitic acid and stearic acid—both saturated fatty acids—become less abundant. In this way, the bone marrow lipids in the legs of reindeer are reminiscent of the brain phospholipids of fish from various climates (see Figure 2.3). The same basic trends exist even in the legs of many tropical mammals. Thus, although the trends are significant for reindeer, they do not seem to be specific adaptations to a truly frigid climate.

Food and nutrition represent great challenges in the environments where reindeer live. Like other deer, reindeer are ruminants. Thus rumen processes, as well as digestive and absorptive processes, play pivotal roles in their physiology of food and nutrition. A key to the survival of reindeer in the Far North is that they eat a great diversity of plants (37 genera were found in the rumens of one herd). Moreover, they obtain an exceptional degree of nutritional benefit from species of lichens ("reindeer moss") and a variety of

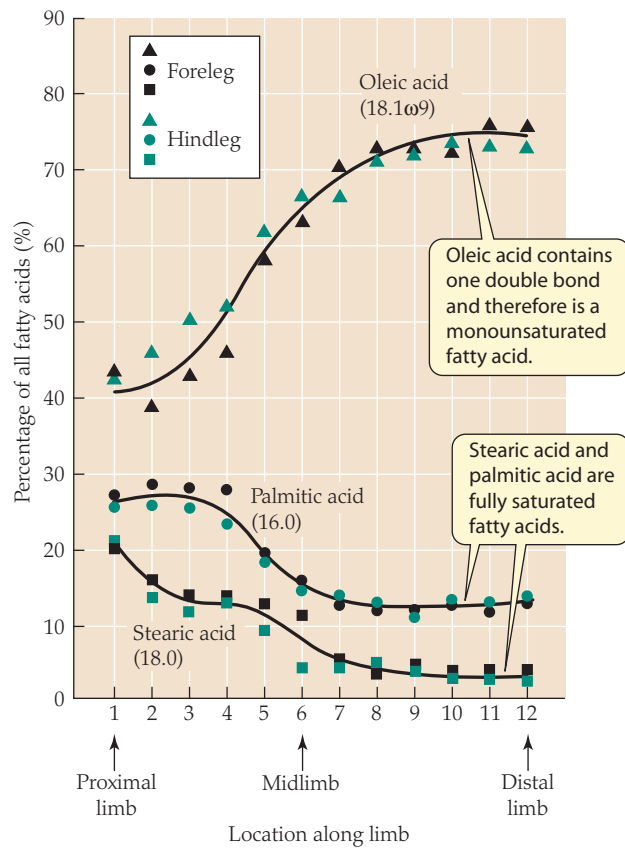


FIGURE 11.3 Fatty acid composition of bone marrow lipids in the legs of reindeer Marrow lipids were sampled at 12 locations from the proximal (upper) end of each limb to the distal (lower) end. The proximal locations were the proximal ends of the humerus and femur; the midlimb locations were the distal ends of the radius and tibia; the distal locations were the third phalanges. In the numbering system for the fatty acids (discussed in Chapter 6, see page 132), the number before the decimal is the number of carbon atoms; that following the decimal is the number of double bonds; and that following ω (omega) designates the position of a key double bond (ω is not written when there are no double bonds). (After Meng et al. 1969.)

that dominate the winter diets of reindeer are collectively the opposite: low in protein, low in minerals, low in highly digestible carbohydrates, and high in cellulose and hemicelluloses. Lichens are often the salvation of reindeer in winter *in terms of supplying energy* because they are abundant, and as we have already said, reindeer can tap a high proportion of their nutrient value. Lichens, however, typify the nutritional problems that reindeer face in winter, in that, being low in protein and low in minerals such as Na^+ , they are not even close to being nutritionally complete. **Figure 11.4**, which summarizes the composition of the foods available to reindeer throughout the year in Finland, is well worth close study, because it illustrates dramatically that animals in the wild—away from veterinarians and manufactured feeds—often face substantial nutritional stresses.

Reindeer and the microbial symbionts in their rumens make adjustments as the seasons change. For instance, certain strains of reindeer fatten dramatically as winter approaches, thereby reducing their need for winter food. In addition, the community of fermenting microbes in the rumen changes in composition in ways that respond to the shifts in the types of foods eaten. **Table 11.1** presents one example, indicating that microbes that digest woody, fibrous plant material (including cellulose and hemicellulose) increase in winter when reindeer ingest considerable amounts of such material. A recent study showed that the mixed rumen microbial community in Norwegian reindeer became four to six times more capable of breaking down lichens when lichens were chronically

other species of far-northern plants that are not much eaten by other mammals.² The exact mechanisms by which reindeer are able to exploit their unusual foods remain poorly known, although studies of ingestion and egestion show, for example, that reindeer obtain twice the nutrient value from lichens as sheep or cows do. Some lichens produce and accumulate toxic phenolic compounds such as usnic acid, raising the question of how reindeer handle these compounds. Recent research points to degradation by specialized rumen microbes. Usnic acid in ingested lichens is evidently fully broken down during rumen processing and never enters the tissues of the reindeer.

The seasonal cycle of plant growth in the Far North is dramatic—not just because winters are cold, but also because of winter darkness (in some places that reindeer occupy, the sun does not rise above the horizon for 3 months in winter). The summer foods of reindeer in most places are collectively high in protein and mineral nutrients, and they are high in the proportion of total carbohydrate that is in readily digestible forms (rather than cellulose or hemicelluloses). By contrast, the lichens and senescent vascular plants

²For simplicity of language, we use the term *plants* in a loose, comprehensive sense to refer to all the photosynthetic organisms that reindeer eat, including lichens and mosses, as well as true plants.

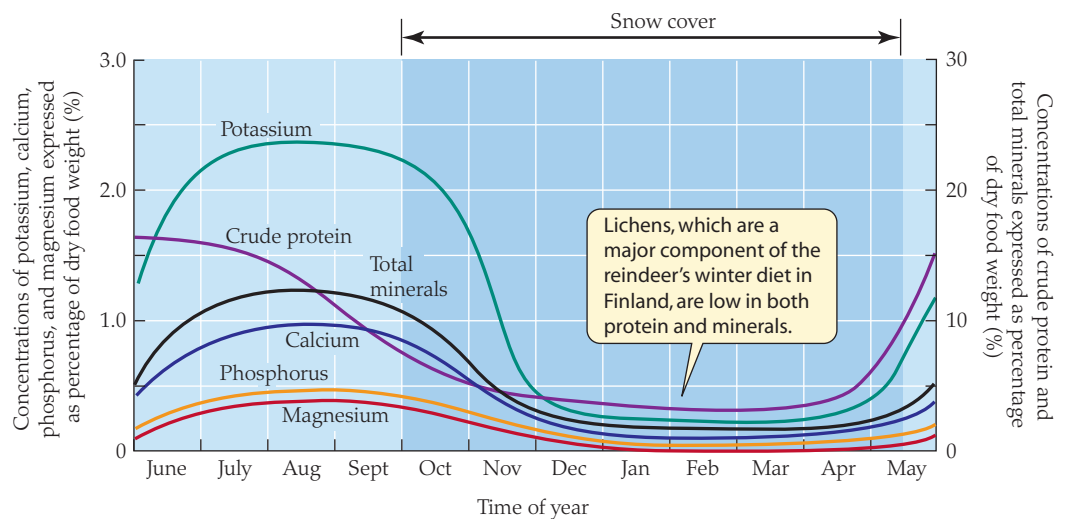


FIGURE 11.4 Seasonal changes in diet: the protein and mineral content of the foods eaten by Finnish reindeer The foods available to—and eaten by—reindeer vary from place to place. The particular seasonal changes seen here are not, therefore, observed everywhere. (After Nieminen 1980.)

TABLE 11.1 Responses of the rumen microbes of reindeer to seasonal changes in diet

The mixed communities of fermenting microbes in rumen fluid were classified using standard microbiological methods. Compared with the summer microbial community, the winter microbial community was more able to ferment plant fiber, including particular structural carbohydrates such as cellulose, and less able to carry out hydrolysis of proteins.

Food breakdown activity	Percentage of microbes that could carry out each activity (%)	
	Summer	Winter
Fiber digestion	31	74
Cellulose digestion	15	35
Hemicellulose (xylan) digestion	30	58
Proteolysis (protein hydrolysis)	51	28
Starch digestion	68	63

Source: After Orpin et al. 1985.

in the diet than when lichens were chronically not eaten. Despite such adjustments, by the time spring arrives after a long winter, reindeer have lost body weight, often are somewhat emaciated, often exhibit other signs of having been in negative nitrogen balance for months, and may exhibit blood mineral levels diagnostic of mineral deficiency. In some places, they are renowned for having high “mineral appetites” in spring.

In addition to the physiological and anatomical features we have already discussed, the distinctive feeding behaviors and migratory behaviors of reindeer herds play key roles in their success in the Far North. Food is thinly distributed there, even for animals that feed on a diversity of plants. Thus herds must range widely to obtain enough food. Reindeer herds are legendary, in general, for being incessantly on the move during daylight hours, covering large areas of ground every day, nibbling as they go. The extraordinary annual migrations of reindeer herds are additional behavioral adaptations, helping them to find not only food but also shelter from wind during winter. Although some herds do not migrate, most do. As winter approaches, the norm is for a herd to migrate about 1000 km from its summer site to its winter site. Some travel farther: Recent satellite-based tracking studies in Alaska and the Yukon revealed that some herds make a round-trip of 5000 km per year. Of all animals that travel by walking or running, reindeer migrate the greatest distances!

The movements of the adults in a herd are a part of reality for all calves born into the herd. Calves must join in the wide-ranging daily movements of their herd soon after birth, as we have already mentioned, and by autumn of their first year of life, they must be ready for the annual migration.

Newborn Reindeer

When reindeer are born, they already have a well-developed pelage, consisting of woolly, hollow hairs. Their fur provides substantial insulation as soon as the uterine fluids have evaporated away and the hairs are dry. From the moment of birth, reindeer also exhibit a typical homeothermic relation between their metabolic rate and the air temperature, as shown by the red line in **Figure 11.5**. Newborns

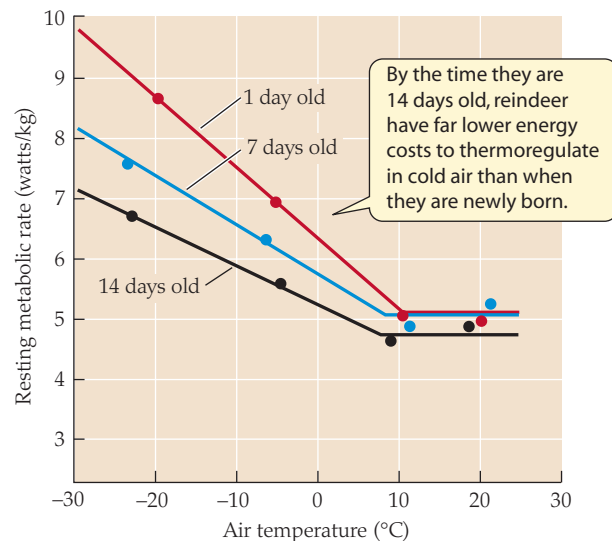


FIGURE 11.5 Resting metabolic rate as a function of air temperature in newborn and growing reindeer The air was still when these measurements were made. Dots are averages for the sets of animals studied at various conditions. (After Markussen et al. 1985.)

are able to raise their rate of metabolic heat production to at least twice their resting rate. By virtue of the combined effects of their pelage insulation and this thermogenic ability, newborns are able to keep their body temperatures at 39–40°C when the air is –20°C to –25°C (a difference of 60°C or more) for at least a few hours in still air. This performance probably represents the pinnacle or near-pinnacle of thermoregulatory ability among all the terrestrial newborns on Earth.³ That said, it remains true that reindeer are born into an environment that can be very harsh, and the thermoregulatory abilities of newborns are far inferior to those of adults. Many newborns die if they get wet from precipitation, or if the wind blows briskly or the air temperature remains very low for a day or more.

Reindeer calves grow rapidly compared with other deer. Partly as a consequence of their increasing body size, their metabolism–temperature relation becomes noticeably more favorable with each passing week (see **Figure 11.5**). When calves are 2 weeks old, the weight-specific rate of heat production that they require to stay warm at an air temperature of –20°C is already reduced to only 70% of that required at birth. For understanding the rapid growth of reindeer calves, it is undoubtedly significant that the milk produced by their mothers is about 20% lipid, compared with about 4% lipid in cow’s milk. Reindeer milk is accordingly very energy dense (see **Table 6.3**), having about three times the energy value per liter as cow’s milk has. It is also particularly rich in protein. The nutrient-rich milk of reindeer aids the rapid growth of the calves. In addition, calves may start eating vegetation within 2–3 days of being born, and by 2 weeks after birth they eat considerable amounts of plants, while continuing to nurse. By late autumn of their first year, when they are 5–6 months old and fully stop nursing, they have reached 50–60% of their adult weight. This extent of growth in the first season of life far exceeds the average for other, related mammals and is believed to be important in enabling young reindeer to participate successfully in their herd’s long migration to its wintering area.

³Newborn muskox (*Ovibos moschatus*) may be superior, partly because of greater body size. At birth, reindeer calves weigh about 4–5 kg, whereas muskox calves weigh about 8 kg (on average, adult muskox are about twice the size of adult reindeer). Newborn muskox have a highly insulating pelage and large deposits of brown fat.

BOX 11.1 KNOCKOUT MICE CLARIFY THE FUNCTION OF BROWN FAT

Molecular genetic tools have been used to produce laboratory mice that cannot synthesize the type of mitochondrial protein, *uncoupling protein 1 (UCP1)*, that mediates nonshivering thermogenesis (NST). The gene coding for UCP1 is inactivated in these mice. As explained in **Box Extension 11.1**, research using these knockout mice has provided strong support for two critical concepts: (1) brown fat is the sole tissue in which NST occurs and (2) UCP1 is the only molecular form of UCP that mediates NST.

A great deal of interest has focused on the mechanisms by which newborn reindeer and other young mammals increase their metabolic heat production for thermoregulation. Nonshivering thermogenesis (NST) by brown fat plays an extraordinary role in this regard. Brown fat is nearly always the principal thermogenic tissue in newborn placental mammals, and NST is thus the principal mechanism of thermogenesis in newborns (**Box 11.1**). *Why* brown fat and NST should be of paramount importance in newborns is largely an unresolved mystery, as we discuss later.

The ways in which brown adipose tissue and NST have been identified in reindeer calves illustrate well the steps that physiologists typically take to identify the tissue and process. The first study indicating that brown fat occurs in newborn reindeer involved microscopic examination of adipose tissues. The investigators observed that the fatty tissue between the scapulae (shoulder blades) of newborn calves is reddish brown and, suspecting it to be brown fat, prepared it for microscopy. The microscopic approach to identifying brown fat is based on the fact that the tissue usually differs from white fat in several structural ways. For example, brown fat is much richer in mitochondria than white fat, and its intracellular fat deposits are multilocular (meaning there are many small lipid droplets per cell) rather than unilocular (one droplet per cell) as in white fat. Microscopic studies performed in about 1980 indicated that *most of the major deposits of adipose tissue in the body of a newborn reindeer are brown fat*. Nonetheless, physiologists assume that function, not just morphology, must ultimately be directly studied for function to be understood. Thus, soon after microscopy had established the likely presence of brown fat in newborn reindeer, investigators tested calves to determine their responses to injected norepinephrine.

As discussed in Chapter 10, thermogenesis by brown fat is ordinarily activated by the sympathetic nervous system, secreting norepinephrine. On the basis of this fact, an animal's response to a norepinephrine injection has often been used as an informative (although relatively crude) test for brown-fat function. When newborn reindeer are injected subcutaneously with a standard dose of norepinephrine, they respond with a large increase in their rate of O_2 consumption (**Figure 11.6**). This response to norepinephrine, coupled with the microscopic observations discussed earlier, convinced physiologists that brown fat and NST are important for heat production in newborn reindeer.

Always, however, thoughtful scientists are wondering if their standards of evidence are adequate. Anyone who has spent

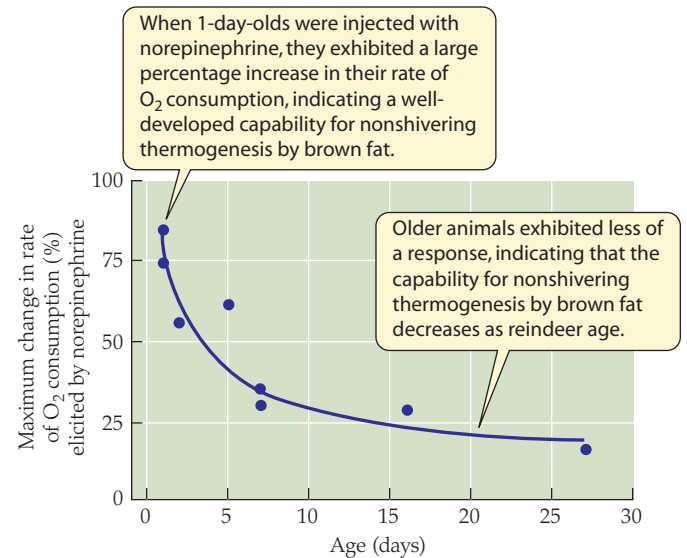


FIGURE 11.6 A test for brown-fat thermogenesis in newborn and growing reindeer Reindeer of various ages were injected subcutaneously with a standard dose of norepinephrine per kilogram of body weight. (After Soppela et al. 1986.)

months of his or her life gathering data becomes aware that there is a risk of being fooled. Maybe, one fears at times, the hard-won data do not say exactly what we have imagined they say. Because of these concerns, people using the microscopic approach kept reassessing whether the microscopic criteria used to identify brown fat were infallible. By the last decade of the twentieth century, these investigators had concluded—from hundreds of studies on brown fat in various mammals—that in fact the traditional microscopic criteria are not 100% reliable. On unusual occasions, when the traditional criteria are used, white fat can seem to be brown fat, or vice versa.

A third test for brown fat was therefore devised. It employed a distinctive molecular marker: the mitochondrial protein *uncoupling protein 1 (UCP1)*, which is believed to occur exclusively (or virtually exclusively) in brown fat, not white fat or other tissues. Antibodies to UCP1 can be produced in a laboratory. Then, UCP1 in a newborn reindeer or other animal can be unambiguously identified by its antigen–antibody reaction (immunocytochemistry). Studies have shown that all of the major adipose-tissue deposits in newborn reindeer react with UCP1 antibodies, demonstrating more convincingly than ever that the tissues are brown fat.

Reindeer newborns are not alone in being well endowed with brown fat. In fact, most placental mammals, including humans (**Figure 11.7**), have extensive masses of brown fat at birth (pigs are exceptions, as discussed in **Box 11.2**). In large-bodied species, such as reindeer and humans, the brown fat of newborns typically declines rapidly with age. This decline is particularly rapid in ruminants. In reindeer, sheep, goats, and other species of ruminants that have been studied, all the brown fat present in newborns undergoes a genetically programmed transformation into white fat by 1 month of age; this is demonstrated by the fact that in 1-month-old animals, the gene for UCP1 is no longer expressed and no tissue reaction with UCP1-specific antibodies occurs. Simultaneously, the metabolic response of the young animals to a norepinephrine injection declines substantially (see **Figure 11.6**).

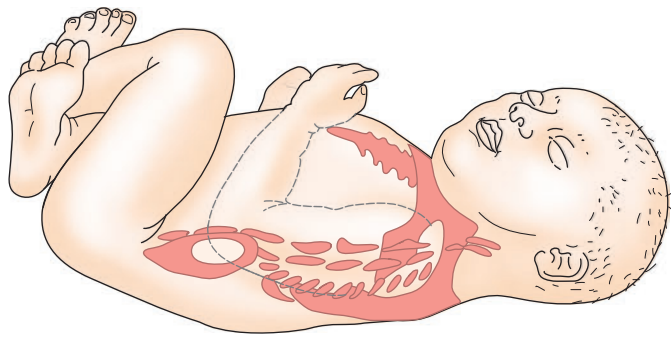


FIGURE 11.7 Brown adipose tissue in a human infant The tissue occurs in discrete masses in many parts of the body. (After Hull 1973.)

In the sorts of species we are discussing, as the capacity of a young mammal for *nonshivering* thermogenesis declines, *shivering* becomes more important as a source of heat production; ultimately, shivering becomes the sole mechanism of increasing heat production for thermoregulation. This transition is quite obvious in people; whereas we rely principally on nonshivering thermogenesis when we are newly born, we become dependent principally on shivering thermogenesis in youth and adulthood. In reindeer, as already said, the transition occurs relatively rapidly. Shivering becomes their only substantial mechanism of increasing metabolic heat production for thermoregulation by the time they are 1 month old, as far as is now known. This is not to say that young reindeer shiver a lot. By the time reindeer are 1 month old, the warm air temperatures of summer have started to prevail, and the need for any sort of thermoregulatory thermogenesis is reduced. When winter arrives,

the young reindeer are 6 months old and—similar to adults—have lower-critical temperatures of about -30°C (see Figure 11.1).

The primary role of brown fat in newborn ruminants, such as reindeer and sheep, seems to be to act as a transition source of heat production: the dominant site of thermogenesis when the animals first make the transition from life in the uterus to life outside their mother. For brown fat to play this role, it must develop extensively prior to birth, a fact that raises numerous interesting questions.

Do fetuses, for example, develop more brown fat when the environment into which they will be born is cold rather than warm? This question has been studied in sheep, in an indirect way, by shearing off the fur of some mothers during their final month of pregnancy and comparing their newborns with the newborns of unshorn mothers (shearing serves in these experiments to mimic colder weather for the mothers by lowering their insulation). Lambs born to shorn mothers have more brown fat at birth than lambs born to unshorn mothers have. Moreover, when newborns are exposed to an air temperature that is chilly for lambs (14°C), the newborns of shorn mothers never shiver, whereas many of the newborns of unshorn mothers shiver. These results indicate that the intrauterine development of brown fat by fetuses is modified, depending on the cold stress experienced by their mothers, in ways that help ensure that NST will be sufficient for thermoregulation in the newly born.

Another interesting question is how the large masses of brown fat in unborn, near-term young are regulated so that they do not catabolize large amounts of the young's foodstuffs. Logic suggests that, prior to birth, a young animal will profit most from the foodstuffs it has by using them to grow and mature; brown fat, if uncontrolled, could turn large quantities of the foodstuffs into heat and chemical wastes. Experiments reveal that if near-term

BOX 11.2 GENOMICS CONFIRMS THAT PIGLETS LACK BROWN FAT

The completion of a partial sequence of the genome of domestic pigs in 2005 set the stage for a remarkable discovery. Investigators located the gene for uncoupling protein 1 (UCP1) in this genome, but when they looked in detail, they found the gene to be disrupted by several mutations and deletions, including complete deletion of two exons. The gene is nonfunctional, a fact that greatly strengthens a conclusion reached through earlier morphological studies, that piglets lack brown fat.

Studies of additional types of pigs quickly revealed that the UCP1 gene is disrupted in all of them. European wild boars, warthogs, red river hogs, and Bornean bearded pigs display the same exon deletions that are observed in domestic pigs.

Phylogenetic analysis indicates that the UCP1 gene became disrupted in the pig lineage about 20 million years ago. As yet, no one can be certain why this occurred. Nor can anyone be certain whether the gene became nonfunctional first and then brown fat disap-



A European wild boar, the only wild pig that lives in cold climates

peared, or vice versa. In any case, members of the pig family today are unusual among mammals in that the newborns lack nonshivering

thermogenesis and depend entirely on shivering for physiological heat production. Piglets tend to be especially vulnerable to cold stress.

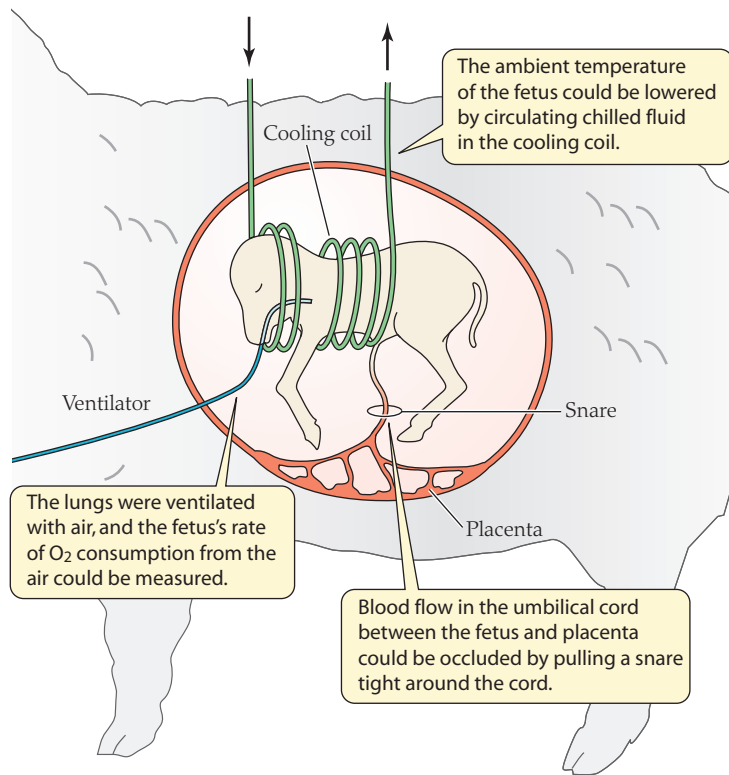


FIGURE 11.8 A near-term sheep fetus in the uterus prepared for study of “simulated birth” (From Power et al. 1987.)

sheep fetuses are cooled inside the uteruses of their mothers (Figure 11.8), they do not activate their brown fat or engage in NST. However, if blood flow from the placenta of a near-term fetus is blocked by pinching shut the umbilical cord, the fetus rapidly exhibits substantial NST. These results and others indicate that a near-term sheep fetus in the uterus receives from its placenta one or more types of signaling molecules (probably prostaglandins) that inhibit its activation of brown fat. These signaling molecules are cut off at birth by the severing of the umbilical cord, and the brown fat is then able to respond vigorously to the chilly outside environment by producing heat! A similar process may occur in reindeer. Future research will tell.

The Future of Reindeer: Timing and Ice

Demographers have sounded an alarm that wild reindeer may be in decline throughout their circumpolar distribution. Since the 1980s, 80% of populations studied have exhibited declines. If we presume that these data represent a long-term trend, the causes are of great interest. Some of the causes may be intimately related to the environmental physiology of the animals in a changing world.

Migratory ungulates commonly have evolved life histories closely synchronized with cycles of plant growth. This phenomenon is very evident in reindeer. As spring unfolds, herds of reindeer migrate back to the areas where they will spend the summer, and after arriving there, the pregnant females in a herd give birth almost synchronously with each other. Historically, births have tended to occur at a time when mothers and young can make maximal use of the peak period of spring plant growth on the summering grounds. For several reasons—one being that when reindeer start

their migration, they are at a distant place from their summering grounds—the question arises, in a changing world, of whether birthing will continue to coincide with peak spring plant growth. A recent study on West Greenland herds indicates that it will not. Over the past 20 years, the peak of spring plant growth has occurred earlier and earlier because of warming spring temperatures. The reindeer, however, have birthed always at about the same time each spring. A growing mismatch of 5–10 days has consequently developed between the time when young are born and the time when food for them is most readily available. As this mismatch has developed, death rates of offspring have risen.

The consequences of this sort of mismatch highlight, among other things, the precariousness of reindeer life history. Reindeer have evolved to be specialists in leading lives of lifelong (“cradle to grave”), direct exposure to an especially harsh environment. That environment is also particularly unforgiving: small changes can impose large consequences. In addition to the mismatch just discussed, another “small” change that may be driving the decline of reindeer populations is the change of snow type. Arctic indigenous peoples often have dozens of words for the forms of ice, snow, and precipitation—reflecting the fact that subtle differences (often unrecognized by non-Arctic people) may be of large importance. Evidence exists that in some areas where reindeer live, precipitation is falling to a greater extent as rain (and a lesser extent as snow) as years go by because of global warming. When precipitation falls as rain, it can freeze on the ground into a hard, thick crust that has been observed to block reindeer from reaching food plants, leading to hunger and starvation.

Thermoregulatory Development: Small Mammals Compared with Large

Mammals the size of mice and rats have only very modest capabilities to thermoregulate when they are first born. The white-footed mouse (*Peromyscus leucopus*), one of the most abundant native small mammals in North America, provides a typical example of the course of development in such animals. The species occurs in northern states such as Michigan and Wisconsin, as well as into Canada. In these areas, the mice give birth to their first litters of young each year in March and April, when the cold of late winter still prevails. Their litters consist of 4–6 young born without fur.

In the days immediately following birth, young white-footed mice can respond to cold exposure by increasing their metabolic rates to a small extent, and if all the young in a litter huddle together within the nest their mother provides, they are able collectively to thermoregulate reasonably well for a few hours even when the air outside the nest is near freezing. A newborn litter, therefore, can stay relatively warm for a while when its mother is away foraging. However, if a single newborn mouse is removed from the nest and studied by itself, it cannot marshal a high enough metabolic rate to stay warm even when the air temperature is +25°C—a temperature higher than “room temperature” in American buildings. At an ambient temperature of 25°C, the body temperature of a solitary 2-day-old soon drops from 37°C to about 28°C—not because the animal is in some sort of controlled hypothermia, but because its thermoregulatory abilities are overwhelmed. The young of lemmings and other small mammals characteristic of the Far North are not much different; to thermoregulate in their first days of life, they

require a protective microhabitat, including the nest their mother provides and their siblings with which they huddle.

The length of the nestling period of white-footed mice is typical of that of most mice and rats: about 3 weeks. During those 3 weeks, young mice must become physiologically capable of setting off on their own. They must, for example, become able to thermoregulate as isolated individuals in the environment outside the nest, however cold that environment may be. As Figure 4.4 shows, individuals dramatically increase their body insulation and the rate at which they can produce heat during their 3 weeks of nestling life. Consequently they become capable of thermoregulating by themselves.

Regarding the *mechanisms* of thermogenesis in developing mice and rats, the evidence available indicates that shivering is not functional in most species for roughly the first week of postnatal life. Brown fat, in contrast, is present at birth. The brown fat grows as the young grow. In fact, studies of laboratory rats have shown that the maturation of brown fat as a thermogenic tissue outpaces body growth for a period during nestling development, so that the brown fat is able to produce ever more heat per unit of body weight as time passes.

Let's focus now on *small* mammals as compared with *large* mammals. The trajectory of brown-fat development in small mammals is extremely different from the trajectory in large mammals. In reindeer and sheep, brown fat is maximally or near maximally developed at birth, and it starts to wane soon after birth, so it is gone or approximately gone by about a month of age. In small mammals such as mice and rats, by contrast, brown fat is far from fully developed at birth, and during much of the first month of life, it develops an ever-greater thermogenic ability. Correlated with these differences in developmental trajectory, the adults of large and small mammals tend to exhibit consistent differences in brown fat. Brown fat is not present to any great extent in the adults of most large-bodied species of mammals.⁴ By contrast, brown fat is conspicuous in the adults of most species of placental mammals smaller than about 5 kg. It becomes a particularly prominent tissue in these adults when they are acclimated to cold or acclimatized to winter, as we saw in Chapter 10; and it is a prominent tissue in hibernators, as we will discuss later in this chapter.

Looking back over our discussion of the development of thermoregulation in large and small species, it is striking to observe that in *both* large and small placental mammals, brown fat and nonshivering thermogenesis are the favored means of producing heat for thermoregulation at birth and during the period immediately following birth. Only rudimentary hypotheses are presently available to explain why nonshivering thermogenesis is emphasized while shivering is not. One hypothesis is that skeletal muscles are inherently too immature at birth for shivering to be a viable primary mechanism of thermogenesis in newborns. Another hypothesis stresses that brown fat is often positioned, on average, deeper in the body than the muscles that shiver; possibly,

⁴Recently, deposits of brown fat “disguised” within white fat have been discovered by use of advanced techniques (e.g., positron emission tomography) in adult humans—after decades in which most specialists had concluded that humans lose brown fat entirely prior to adulthood. The physiological significance of these adult deposits has yet to be determined. Their function may be in body-weight regulation or control of blood glucose rather than thermoregulation. The discovery of these deposits raises the question of whether brown fat will be found to some extent in adults of other large-bodied mammals when the same advanced techniques used in the recent study of people are applied to other species.

therefore, natural selection has favored nonshivering thermogenesis in newborns because it delivers heat more effectively to the body core than shivering could. Neither of these hypotheses has been tested, and both make unverified assumptions. Thus the question of why newborn placental mammals so consistently use brown fat and nonshivering thermogenesis to produce heat remains a tantalizing challenge for future research. The fact that we humans rely on brown fat for thermogenesis when we are newly born adds interest to finding an answer.

The Effect of Body Size on Mammals' Lives in Cold Environments: An Overview

A retrospective look at the topics we have discussed so far in this chapter makes clear that body size is a principal determinant of the options available to mammals for thermoregulation. Although both reindeer and white-footed mice are warm in the days following their birth, they are warm for different reasons. Newborn reindeer are so large that they have few options for using protective microhabitats; they cannot burrow underground, and on the tundra they cannot readily find other refuges. Thus newborn reindeer must *physiologically* confront the full harshness of their environment if they are to stay warm. Fortunately, large size—while limiting behavioral options—has physiological advantages; because of their size, newborn reindeer have a surface-to-volume ratio that is favorable for retaining heat in cold environments, and they can have a thick pelage. The interplay between behavior and physiology is almost opposite for small-bodied newborns such as white-footed mice. They are smaller than the little fingers on our hands, and just as naked. Thus, physiologically there is no chance that newborn mice could evolve mechanisms that would allow them to thermoregulate while fully exposed to a cold external environment. Being small, however, they can exist in highly protective microhabitats; their mothers can place them in secluded, benign locations such as underground burrows and can readily ensconce them in an insulating nest. The reasons newborn white-footed mice are warm are principally behavioral: When their mother is present, the newborns are warmed by her; and when she is absent, they benefit from the behavioral provisions she has made for them.

The same trade-offs between physiology and behavior are equally evident in the lives of adult mammals. During winter in Earth's frigid places, small nonhibernating mammals such as lemmings in the Arctic and pikas in the high mountains are able to escape the biting cold and howling winds of the larger environment by living under the snow (see Figure 1.17) or in other protective hideaways. Their ability to escape in this way is fortunate because, physiologically, a mouse- or rat-sized adult could not survive full exposure to the cold of winter in such places. Large mammals, in contrast, are in a far more advantageous position in terms of their physiology of thermoregulation; the body size of an adult reindeer is one of the major reasons it can have a lower-critical temperature below -30°C . The physiological advantage of large size is itself fortunate, because large size limits behavioral options. A large mammal, such as an adult reindeer in the Arctic or a bighorn sheep in the high mountains, cannot escape the severity of the cold season by burrowing under the snow.

The single greatest behavioral option for large-bodied species is migration. In fact, as we saw in Chapter 9 (see Figure 9.8), migra-

tion is energetically more feasible for large species than for small ones. Often, therefore, with the approach of winter, as the small mammals in a place go underground or under the snow, the large ones get out. Bighorn sheep trek to the lowlands, and reindeer often migrate into more-forested areas where they can find windbreaks, as well as better winter feeding grounds.

Because body size is one of an animal's most consequential attributes, it is rewarding to ponder the pros and cons of different sizes. If natural selection starts to favor an increase or decrease in the body size of a species, what are all the implications, and the potential trade-offs, over the full span of an animal's life? We have touched on only some of the highpoints in our discussion here.⁵

Hibernation as a Winter Strategy: New Directions and Discoveries

The hibernating species of placental mammals are noted for retaining brown fat as adults. Indeed, when Conrad Gessner first described brown fat in 1551, he was studying the adults of a hibernating species, the European marmot. For four centuries thereafter, brown fat was observed in the adults of one hibernating species after another. The association of brown fat with hibernation was so consistent, in fact, that—although the function of brown fat was unknown—the tissue was dubbed “the hibernation gland.” The actual function of brown fat—not a gland but a thermogenic tissue—was not discovered until the mid-twentieth century.

Today we know that in adult hibernators, brown fat is the *thermogenic tissue that takes the lead in rewarming during arousal* (emergence from hibernation). Intense thermogenesis by brown fat is activated at the very beginning of the arousal process. Because of the placement of brown fat in the body (some deposits actually surround major arteries), and because of blood flow patterns, heat produced by the activation of brown fat is believed to be delivered particularly to the vital organs such as the heart, lungs, and brain. This focused warming of the vital organs, starting early in arousal, may be important in poising those organs to play their roles (e.g., coordination mediated by the brain) in the overall sequence of events by which homeothermy is gradually restored throughout the body.

As we discuss hibernators further, two species will receive special attention, the Arctic ground squirrel (*Urocitellus parryii*) and the alpine marmot (*Marmota marmota*). The ground squirrel, which weighs 500–800 g, is found widely in the Far North—Alaska, the Yukon, and neighboring parts of Canada. The marmot, which is larger and weighs about 4–5 kg, occurs high in the European Alps. Both species employ hibernation as a strategy to cope with the stresses of winter in some of Earth's most frigid places.

The great majority of hibernators have adult body sizes of 5 kg or less. This means that alpine marmots are near the upper limit of the size range that typifies most hibernators. Typically, species of

mammals larger than 5 kg that occupy frigid environments, such as reindeer, remain active and fully homeothermic through all seasons (although some exhibit nonhibernation hypothermic or hypometabolic states at times). Physiologists have pondered why most large-bodied species have not evolved hibernation. One reason is probably that the energy savings afforded by hibernation decline with body size. As shown in **Figure 11.9**, the weight-specific metabolic rates of hibernators in hibernation are statistically the same regardless of their body size. However, when the animals are not hibernating, small-bodied species have higher weight-specific metabolic rates than large-bodied species. Thus the energy savings achieved by hibernation decrease as body size increases. In the face of this allometric trend, natural selection seems not often to have favored the evolution of hibernation in large-bodied species. Bears stand out as a dramatic exception.

Among species of mammals that weigh 5 kg or less, hibernation is not at all universal. In the Arctic, for example, whereas ground squirrels hibernate, lemmings and flying squirrels do not. We do not understand why species have diverged in these ways. At our present level of understanding, we can only conclude that the two modes of dealing with the cold of winter—hibernating and staying active—must each have pros and cons for small and medium-sized mammals. Neither strategy is so obviously “better” that it has become universal.

As we discuss Arctic ground squirrels, alpine marmots, and other hibernators, it is worth reflecting on the fact that much of what we know about them today is a consequence of a technological revolution that has occurred in the last 40 years in which biologists, engineers, and computer scientists have teamed up to create ever-better technologies for the remote monitoring of physiological traits. At the beginning of this revolution, small radio transmitters were designed that could be implanted in animals and report

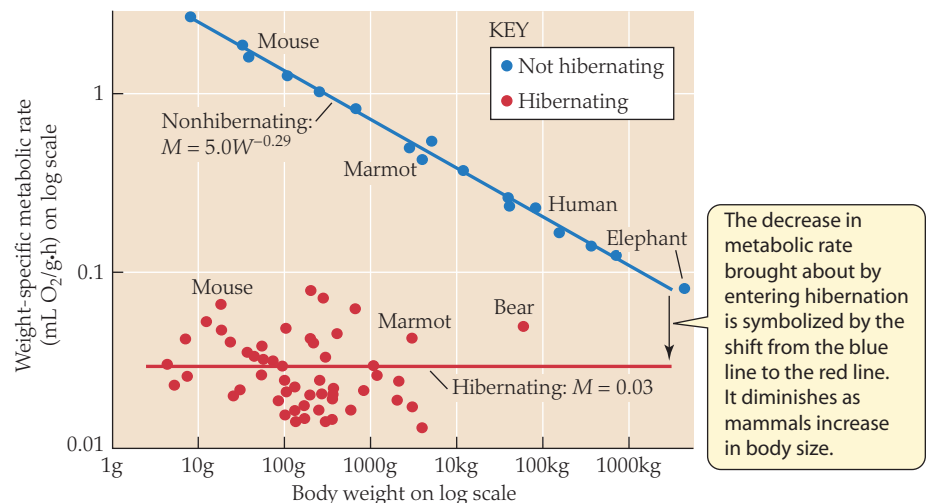


FIGURE 11.9 The allometry of energy savings by hibernators Weight-specific resting metabolic rate is shown as a function of body weight in nonhibernating and hibernating mammals, on log–log coordinates. The blue line shows the relation in nonhibernating mammals; this metabolic rate decreases substantially as body weight increases. The red line shows the relation in hibernating mammals; this metabolic rate is statistically the same for animals of all body weights. The nonhibernating metabolic rates are basal rates. Hibernating metabolic rates were measured at ambient temperatures of 2–7°C. In the equations describing the two lines, M is weight-specific metabolic rate ($\text{mL O}_2/\text{g}\cdot\text{h}$); W is body weight (g). (After Heldmaier et al. 2004.)

⁵The basic theme—that large body size tends, overall, to be a physiological advantage, whereas small body size tends overall to be a behavioral advantage—is also evident in desert mammals, as discussed in Chapters 28 and 30 (e.g., see Figure 30.1).

body temperatures by *radiotelemetry*. Today's transmitters are able to operate on their built-in battery power for many continuous months, and the data they transmit are recorded automatically by computers. A more-recent advance is the introduction of *data loggers* to physiological research. These are dedicated microcomputers that have large amounts of internal memory and that periodically log the temperatures they measure into memory.

With these advances in technology, records like that in **Figure 11.10** have become possible—and have revolutionized knowledge of the physiology of hibernation. The record in the figure shows the body temperature of a *free-living* and *undisturbed* Arctic ground squirrel for *8 continuous months*—the full duration of its hibernation season!

Arctic ground squirrels supercool during hibernation and arouse periodically throughout their hibernation season

Although most hibernating species spend the winter in microhabitats where the temperature always stays above freezing, Arctic ground squirrels cannot do so over much of the range where the species occurs. The reason is *permafrost*—soil that never melts throughout the year. At the Arctic Circle, permafrost starts at 0.8–1.0 m below the ground surface. The ground squirrels can burrow only in unfrozen soil, and only the soil above the permafrost thaws in the summer. Accordingly, the animals cannot burrow deeper than about 1 m. At that depth the ambient temperature in the winter can drop to far below freezing, even sometimes to -25°C , within the **hibernacula** (singular *hibernaculum*) of the squirrels—the chambers or cavities where they hibernate.

As mentioned in Chapter 10, essentially all hibernating species periodically undergo temporary arousals during their hibernation season. The animals typically remain in their hibernacula during these arousals. This behavior explains why early naturalists believed that hibernation simply started in the early winter and ended in the spring; hibernating animals disappeared into their hibernacula for the entire period. When automated long-term records of the body temperatures of hibernators were obtained, however, they revealed that periodic arousals almost universally occur. The Arctic ground squirrel in **Figure 11.10** aroused 11 times between October and April before it aroused for the final time and emerged from hibernation. Continuous periods of hypothermia lasted 1–3 weeks. Between those bouts of hibernation, the ground squirrel raised its body temperature to $36\text{--}37^{\circ}\text{C}$ for 12–24 h during each arousal.

A striking aspect of the record in **Figure 11.10** is that, by early December, the ground squirrel's body temperature fell below 0°C during periods of hypothermia! The soil temperature fell as winter progressed, and as the soil temperature fell, the ground squirrel maintained a larger difference between its body temperature during hypothermia and the soil temperature. Nonetheless, the body temperature fell below 0°C , a very unusual state for hibernators. The freezing point of the body fluids of Arctic ground squirrels remains the same during winter as it is in summer: -0.6°C (the typical value for mammals). Yet Arctic ground squirrels sometimes cool during hibernation to body temperatures of -2°C to -3°C . They do not freeze at these times. Instead, they supercool, just as some poikilotherms do in winter (see page 247).

Although supercooling is important, the *principal* way that Arctic ground squirrels cope with the threat of freezing during their hibernation bouts is by *thermoregulating* at body temperatures of -2°C to -3°C ,

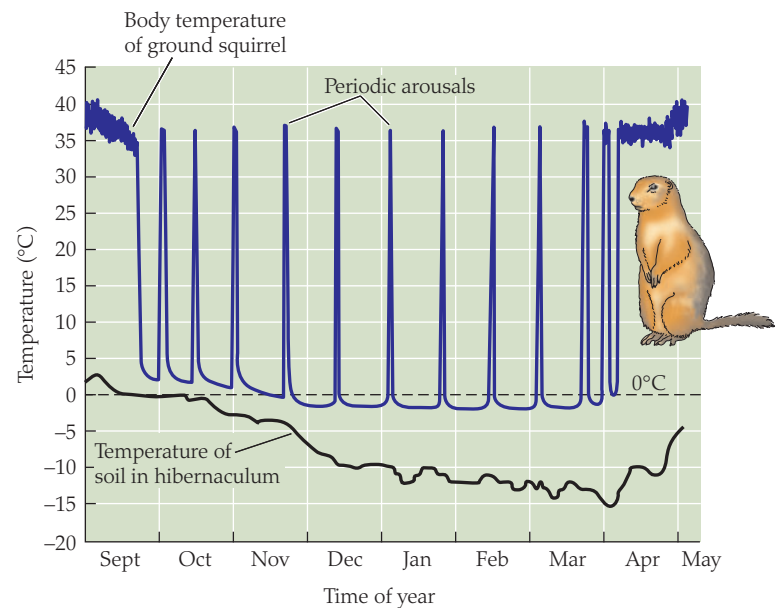


FIGURE 11.10 The body temperature of an Arctic ground squirrel during its hibernation season in Alaska. The body temperature was recorded with a data logger. The soil temperature of the ground squirrel's hibernaculum is also shown. (From Boyer and Barnes 1999.)

thereby maintaining their tissues well above the soil temperature when the soil becomes profoundly cold. By midwinter, for example, the ground squirrel in **Figure 11.10** kept its body temperature 10°C above the soil temperature during its bouts of hibernation. To be endothermic in this way, hibernating Arctic ground squirrels must increase their rates of heat production in midwinter to rates above those seen at other times—such as September and October—when the soil is warmer and they can simply let their body temperature approximate soil temperature. The rate of heat production of a hibernating ground squirrel is increased, as needed, by brown-fat thermogenesis (**Figure 11.11**). As noted in Chapter 10, it is common for mammals and birds that are in states of controlled hypothermia to prevent their body temperatures from falling lower than certain levels by elevating metabolic heat production. The increased energy expenditure lowers the energy savings of hibernation, however.

The composition of the lipids consumed before hibernation affects the dynamics of hibernation

As stressed in Chapter 6, the composition of the foods that animals eat is often as significant as the amount of food. A dramatic illustration of the interaction between food composition and physiology has emerged in recent years from studies of hibernators. In addition to brown fat, hibernators often accumulate large stores of white fat with the approach of winter. The white fat is a storage tissue; lipids are deposited in the tissue as fattening occurs and later are mobilized from the tissue to meet metabolic needs (including the need to replenish lipids oxidized in brown fat). The lipids stored are triacylglycerols (see **Figure 6.4c**) and thus meet the chemist's definition of fats and oils. They are accumulated in droplets within specialized cells called *adipocytes*.

Fattening requires time—often many months. Accordingly, it must be set in motion by cues or processes that occur well in advance of winter stresses. In some species, the primary controls of fattening are photoperiodic; the shortening of day length in autumn, for example, may serve as a cue for fattening to begin. In other species,

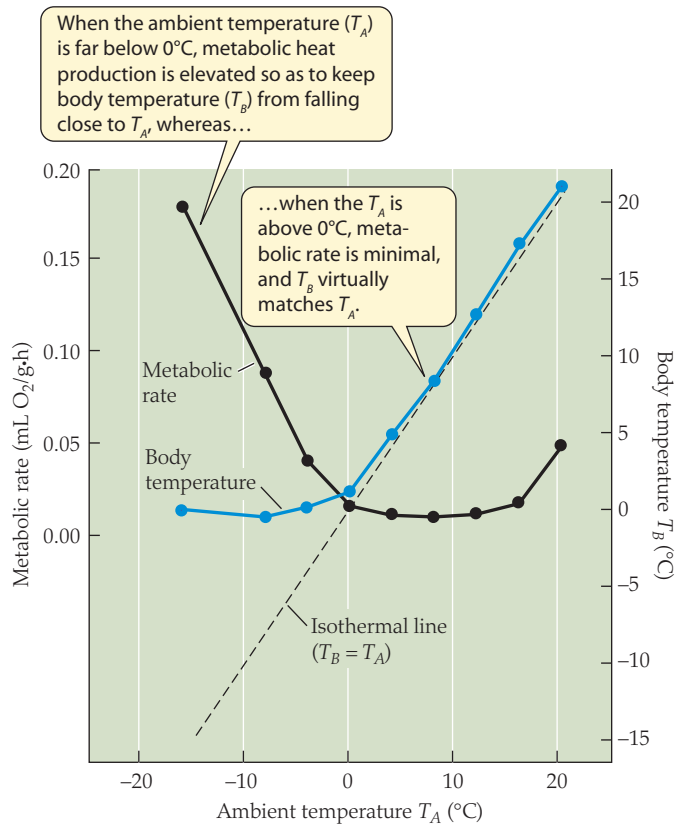


FIGURE 11.11 Excessively low body temperatures are prevented during hibernation bouts by elevated metabolic heat production The plot—which has a scale for metabolic rate on the left and a scale for body temperature on the right—shows the relations among metabolic rate, body temperature, and ambient temperature in Arctic ground squirrels during bouts of hibernation. As the ambient temperature drops from 0°C to -20°C, the body temperature is held higher and higher above ambient because of ever-accelerating metabolic heat production. The isothermal line is a line of equality between body temperature (T_B) and ambient temperature (T_A). (After Barnes and Buck 2000.)

the timing of fattening is endogenously programmed (see Figure 6.25) under control of a circannual biological clock (see Chapter 15).

The storage lipids of hibernators (and other mammals) reflect in their composition the suites of fatty acids present in the foods the animals eat during fattening. Each triacylglycerol molecule is built from three fatty acid molecules (see Figure 6.4c). The fatty acids fall into three chemical categories (see page 132). *Saturated fatty acids*, also termed *SFAs*, contain no carbon–carbon double bonds. *Monounsaturated fatty acids*—*MUFAs*—contain one carbon–carbon double bond per molecule. Finally, *polyunsaturated*

fatty acids—*PUFAs*—contain two or more such double bonds per molecule. As we discussed in Chapter 6, mammals are incapable of synthesizing most PUFAs from scratch. However, if they eat plants rich in PUFAs, mammals can use those PUFAs directly or employ them as substrates for the synthesis of other PUFAs. Because of this relationship, animals that eat foods rich in PUFAs typically deposit fats that are richer in PUFAs than are the fats deposited by animals eating PUFA-poor foods. Similarly, individuals that eat MUFA-rich diets tend to deposit MUFA-rich fats.

Biochemists postulated years ago that storage fats must be in a physically fluid state to be capable of being mobilized and metabolized. If this is true, fats composed primarily of saturated fatty acids could become useless during hibernation because the body temperatures of hibernators are often low enough to cause SFA-rich fats to solidify (for a mental image, recall the hardness of the SFA-rich fats of beefsteaks at refrigerator temperature). Reasoning from these thoughts, researchers hypothesized that hibernators might hibernate in a more effective manner if they deposit fats rich in PUFAs and MUFAs during their fattening periods. Such fats tend to remain fluid at far colder temperatures than fats composed strictly of SFAs (see page 246).

A great deal of evidence now exists indicating that the lipid composition of the diet of hibernators affects the dynamics of their hibernation! Relatively high levels of PUFAs (and sometimes MUFAs) in the diet, as predicted, improve the effectiveness of hibernation. Laboratory studies using defined diets provide one sort of evidence supporting this conclusion. For example, chipmunks in one study were fed three diets: a particularly PUFA-rich diet, an intermediate diet, and a particularly SFA-rich diet. Those on the PUFA-rich diet, compared with those on the SFA-rich diet, were more likely to hibernate, tolerated lower body temperatures, had lower metabolic rates, and had longer bouts of hibernation (meaning they aroused less frequently) (Table 11.2). For evaluating the predicted relation between diet and hibernation, another sort of approach has been to look at correlations between white-fat composition and hibernation performance in free-living animals in the wild, as we will discuss shortly.

Whereas there are many studies by now that demonstrate a relation between hibernation performance and diet (e.g., Table 11.2), these studies do not in fact demonstrate that lipid fluidity is the *reason* for the relation, as originally postulated. At the present time, a cutting-edge in this area of research is that investigators are starting to do detailed studies to determine the *mechanisms* by which diet—and the fatty-acid composition of an animal's fat—

TABLE 11.2 Hibernation performance in chipmunks (*Eutamias amoenus*) fed three diets

All values are means. All differences between the group on a PUFA-rich diet and the group on a SFA-rich diet are statistically significant.

Diet	Percentage that hibernated (%)	Lowest body temperature that did not provoke arousal (°C)	Rate of O ₂ consumption at an ambient temperature of 2°C (mL O ₂ /g·h)	Length of each continuous hibernation bout at an ambient temperature of 5°C (hours)
PUFA-rich	100	0.6	0.034	138
Intermediate	100	1.2	0.047	110
SFA-rich	75	2.2	0.064	92

Source: After Geiser and Kenagy 1987.

affect hibernation. These studies suggest that, whereas lipid fluidity is a factor, other factors are also important.

There are two major types of PUFAs: the omega-3 and omega-6 fatty acids (see page 132). These differ considerably in structure and conformation, as seen in **Figure 11.12**. Recent research indicates that the type of PUFA deposited in white fat sometimes matters, not just the total amount of all PUFAs.

In free-living populations of alpine marmots, because individuals eat different foods, they differ in the amounts and types of PUFAs in their white fat when they start the hibernation season. Individuals with high percentages of PUFAs tend to be more-effective hibernators; they have lower body temperatures during hibernation and lose less weight during the winter than do individuals with lower percentages of PUFAs—confirming the same sort of conclusion as Table 11.2. Closer analysis reveals, however, that this relation is in fact chemically specific. It depends on the percentages of omega-6 PUFAs rather than omega-3 PUFAs.

To explain the relation between omega-6 PUFAs and hibernation success, a current working hypothesis is that when dietary omega-6 PUFAs are incorporated into membrane phospholipids, they provide a superior membrane lipid matrix for the function at low temperatures of key membrane proteins. One of these, a Ca^{2+} -pumping protein, is critical for heart contraction. According to this hypothesis, therefore, adequate omega-6 PUFAs from an animal's food help ensure stable heart action when the heart is cold.

Although periodic arousals detract from the energy savings of hibernation, their function is unknown

Periodic arousals significantly reduce the energy savings of hibernation. To illustrate, let's look at calculations done by Lawrence Wang for Richardson's ground squirrels (*Urocitellus richardsonii*)

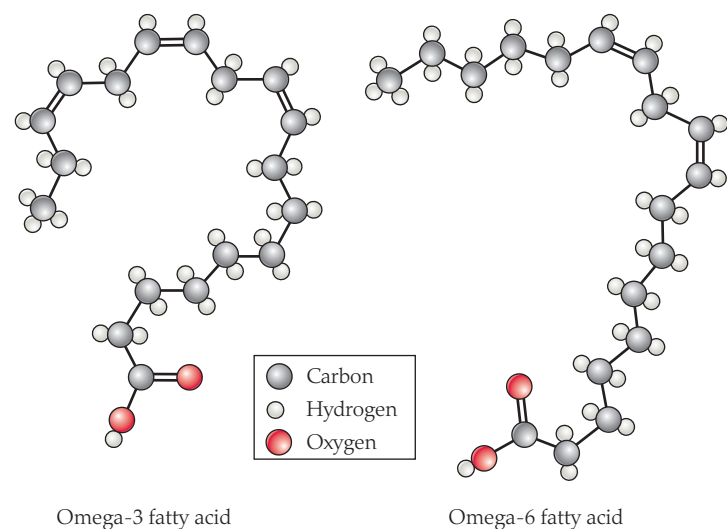


FIGURE 11.12 Structure and conformation of representative omega-3 and omega-6 polyunsaturated fatty acids The particular fatty acids shown are α -linolenic acid (omega-3) and linoleic acid (omega-6); these are the simplest precursors of the two types of PUFAs. Because their structures and conformations are different, the two types of PUFAs, when incorporated into membrane phospholipids, have different effects on the structure of the lipid matrix and create a different context for the function of membrane proteins. (After Ruf and Arnold 2008.)

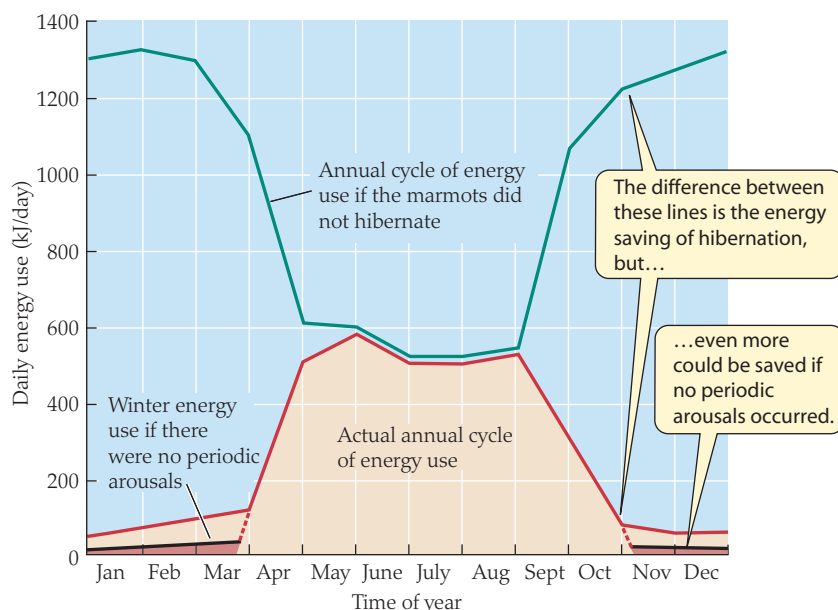


FIGURE 11.13 The annual cycle of energy use in alpine marmots (red line) Also shown are the cycle of energy use that would exist if the marmots did not hibernate (green line), and the energy costs in winter if the marmots did not undergo periodic arousals during hibernation (black lines). (After Heldmaier 1993.)

hibernating in Alberta, Canada. Suppose that these ground squirrels would use 100 units of energy over the course of their winter hibernation season if they did not hibernate. They actually use 12 units of energy. However, of the 12 units they use during the hibernation season, more than 80% is used for periodic arousals!

A qualitatively similar pattern is exhibited by other species. Alpine marmots, for example, reap great energy rewards by entering hibernation each winter (**Figure 11.13**). However, about two-thirds of their energy expenditure during their hibernation period is for arousals, and thus their winter energy expenditure would be only one-third as great if they did not undergo periodic arousals.

Given that animals pay an energy price for periodic arousals, it seems that the arousals must have important functions. In the early days of research on this topic, a lively hypothesis for periodic arousals was that they allow hibernators to void wastes. Investigators assumed, for instance, that the nitrogenous waste product urea accumulates during bouts of hibernation, and thus animals need to wake up to urinate. One piece of contrary evidence that came to light when researchers tested the hypothesis is that in golden-mantled ground squirrels, blood urea concentration does not increase, but *declines*, during a bout of hibernation! Several other seemingly obvious explanations for periodic arousals have also proved to be far from obvious when studied.

In the last 20 years, multidisciplinary attention has been focused on the question of periodic arousals, and several innovative new hypotheses have been put forward. The first of these was that hibernators are unable to sleep when in hibernation and thus must wake up periodically to catch up on sleep. The “sleep” that hibernators often show after arousal, however, has turned out not to be typical sleep, and studies of brain function have lately suggested that in

fact other brain processes are actually occurring. One postulate that has some experimental support is that brain dendrites tend to be lost—and synapses tend to deteriorate—during hypothermia, and arousal is required to restore dendrites and synapses. An entirely different line of thinking—again with some experimental support—is that normal immune responses may be downregulated or blocked during hypothermia. Periodic arousals, according to this hypothesis, allow periodic function of the immune system and thereby enable hibernators to combat pathogenic organisms during the hibernation season.

The intersection of sociobiology and hibernation physiology

Recent analyses of data from many species have established that hibernation is correlated with increased survival in the wild. For example, one question of interest is whether individuals capable of hibernation enjoy lower odds of death during months when they are hibernating than when they are not. In this regard, the available data provide an emphatic answer. On average, in species of hibernating small mammals, an individual is about five times more likely to die in a month when it is active than when it is hibernating. Hibernation probably has this effect mostly because of avoidance of predators; hibernating animals remain always in their hibernacula, instead of moving around in the larger environment where predators can spot them. Avoidance of predation may, in fact, have been a significant factor in the evolution of hibernation. Because of its effect on odds of survival, hibernation can affect an animal's odds of reproduction.

Many additional, interesting questions arise at the interface of hibernation biology and reproductive biology. For example, are hibernation and pregnancy compatible? Do they occur synchronously in the life of an animal? In 2006, researchers reported for the first time that they had observed full-blown hibernation during pregnancy in a placental mammal. Specifically, they had observed three insectivorous bats (hoary bats, *Lasiurus cinereus*) in advanced pregnancy enter deep hibernation for 3–6 days during cold late-spring weather. The bats later aroused normally and gave birth. Prior to this observation on the bats, scattered pieces of less-conclusive evidence—pointing to occasional hypothermia during pregnancy—had accumulated despite the traditional assumption of biologists that pregnant mothers would not enter hibernation. It is clear that hibernation and other forms of hypothermia are less likely to occur during pregnancy than otherwise. Equally clearly, however, we now know that pregnant mothers do sometimes hibernate. When a pregnant female is hypothermic, growth of her young is slowed. On the other hand, she might use hibernation as a mechanism of surviving to term when confronted with a transitory crisis in her food supply. More research will be needed to understand these elusive phenomena.

Male ground squirrels illustrate another consideration that arises in some cases at the interface of hibernation biology and reproductive biology. In ground squirrel species that have been studied, the testicles are regressed during hibernation; and from what is known, no regrowth is possible while hypothermia continues. **Figure 11.14** shows this phenomenon in male golden-mantled ground squirrels. Testicular development starts only after high body temperatures have been restored following the end of hibernation, and because full development requires several weeks, males are unable to breed

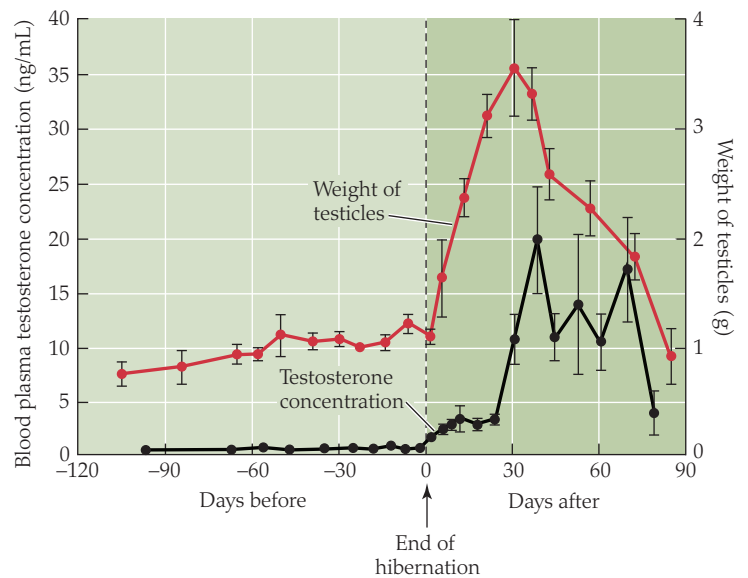


FIGURE 11.14 A constraint of hibernation: Testicular development in ground squirrels requires that hibernation end. Shown are testicular size (weight) and blood testosterone as functions of time before and after the end of hibernation in adult male golden-mantled ground squirrels (*Callospermophilus lateralis*). Error bars show the standard errors. (After Barnes 1996.)

until long after they have terminated hibernation. Why the testicles face these limits is unknown. However, the limits have very real consequences for reproduction. In wild populations of ground squirrels, the males emerge from hibernation many weeks before the females. This early emergence of the males seems necessary for them to prepare to be successful mates.

Social hibernation is another theme of considerable interest. During social hibernation, individuals hibernate together in social groups. Although ground squirrels hibernate as isolated individuals, many of the world's 14 species of marmots undergo social hibernation. Alpine marmots, for example, live throughout the year in social groups. A typical social group of alpine marmots consists of a dominant male and female and an assemblage of related, younger animals of various ages (up to several years old). All these animals hibernate together, in sets that number up to 20 individuals.

Social hibernation in alpine marmots has been shown to increase each individual's probability of overwinter survival, particularly among the young-of-the-year, termed *juveniles*. One reason that survival is aided relates to the fact that these marmots do not allow their body temperatures to go below 3–4°C in winter, yet temperatures in their hibernacula are often lower, meaning that hibernating animals must elevate their metabolic rates to keep their body temperatures from going too low. Animals huddled together in a large cluster are better insulated and require less of an increase in metabolic rate than those hibernating alone or in small groups.

One of the most remarkable revelations in the recent annals of the radiotelemetric study of hibernation is the discovery that adults and subadults in a hibernating group of alpine marmots usually undergo their periodic arousals in close synchrony (**Figure 11.15**). This synchrony lowers their mutual energy costs to arouse. If a single adult were to arouse alone within a hibernating group, it would experience heightened energy costs by being in the group,

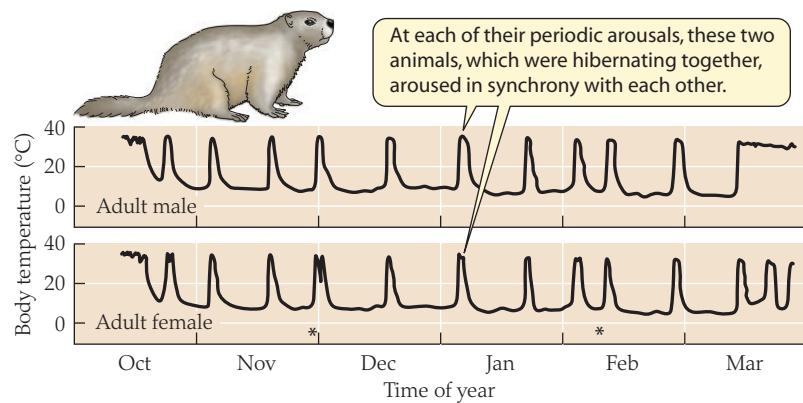


FIGURE 11.15 Alpine marmots arouse synchronously Shown are the body temperatures of two adult alpine marmots that were hibernating together. Outside disturbances may have affected arousal of the animals at the two times marked with asterisks (*). (After Arnold 1988.)

because the cold tissues of the other animals in the group, pressed closely against it, would increase the heat production it would require to raise its own body temperature. What actually happens is diametrically opposite. Adults and subadults in a group arouse simultaneously, thereby lowering each other's energy costs to arouse by mutually warming each other. The simultaneity of this arousal is particularly intriguing because all the animals are hibernating and therefore are seemingly comatose when they initiate the process!

Juveniles in a hibernating group often do not initiate their arousals simultaneously with the adults and subadults, but instead lag behind, letting the older animals warm them for a number of hours (or even days). Only after receiving this benefit do the juveniles invest their own energy in the arousal process.

By statistical calculations, an *index of synchrony* can be calculated for arousals in groups of marmots. A high index for a hibernating group means that the individuals monitored with radiotelemeters in the group aroused highly synchronously. Based on data for 14

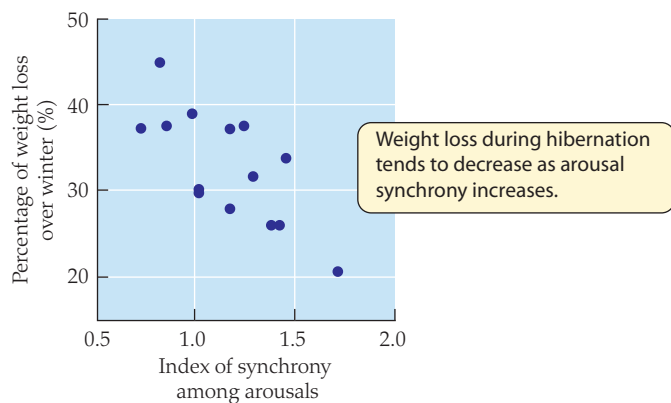


FIGURE 11.16 Weight loss during hibernation as a function of arousal synchrony in hibernating groups of alpine marmots Each point refers to a distinct group of hibernating marmots and shows both the group's average weight loss during winter and the group's degree of arousal synchrony. High values of the index of synchrony signify high degrees of arousal synchronization among group members. (After Ruf and Arnold 2000.)

hibernating groups, **Figure 11.16** shows the relation between loss of body weight and synchrony. As you can see, individuals in highly synchronized groups lost approximately 20–25% of their body weight during the winter hibernation season, but individuals in some poorly synchronized groups lost about 40–45%—roughly twice as much. Because relatively great loss of body weight lowers animals' likelihood of survival, this analysis reveals that synchrony during periodic arousals has important survival consequences.

Further analysis of the data available also reveals that the presence of juveniles is very important in determining the dynamics of group hibernation. When juveniles are present in a group, they themselves have greater chances of survival than if they lived alone. However, because they tend to diminish arousal synchrony by delaying their own arousals relative to others in their group, they increase the amount of weight lost by adults and subadults in their group, and therefore decrease the odds of survival of the older animals. The interplay between sociobiology and hibernation biology is particularly vivid in this context. For an individual adult to survive the winter, avoidance of all contact with juveniles during hibernation would be an advantage. Without immortality, however, adults require juveniles if they are to pass genes to future generations, even though when they associate with juveniles during hibernation, their own odds of individual survival go down.

Study Questions

1. What are the relative advantages and disadvantages of large and small body size in frigid places? In your explanation, try to go beyond the points mentioned in this chapter.
2. When the composition of the community of rumen microbes in a ruminant changes, there are several possible causes. What are some of them? Could you do experiments to decide what the actual causes are? Explain.
3. Long migrations such as those of reindeer are rare in animals that walk across the land, despite being common in flying birds. In what relevant way are reindeer similar to birds in their energetics of covering distance? (Review Chapter 9 if you are stumped.)
4. List possible hypotheses for the function of periodic arousal, and design experiments to test your hypotheses as rigorously as possible.

Go to [sites.sinauer.com/animalphys3e](https://www.sinauer.com/animalphys3e) for box extensions, quizzes, flashcards, and other resources.

References

- Barnes, B. M., and H. V. Carey (eds.). 2004. *Life in the Cold. Evolution, Mechanisms, Adaptation, and Application*. Biological Papers of the University of Alaska, Institute of Arctic Biology, Fairbanks, AK. This is the symposium volume for the 12th International Hibernation Symposium. As such, it provides up-to-date articles, as well as links to the wider literature, in most areas of hibernation research.
- Blix, A. S. 2005. *Arctic Animals and Their Adaptations to Life on the Edge*. Tapir Academic Press, Trondheim, Norway. A unique treasure trove of knowledge about Arctic animals of all kinds, written by a top Arctic physiologist.

- Boyer, B. B., and B. M. Barnes. 1999. Molecular and metabolic aspects of mammalian hibernation. *BioScience* 49: 713–724. A very accessible treatment of many of the current issues in hibernation research, including modification of gene expression.
- Geiser, F. 2004. Metabolic rate and body temperature reduction during hibernation and daily torpor. *Annu. Rev. Physiol.* 66: 239–274. A detailed exploration of several key themes in modern research on the comparative biology of hibernation and other hypothermic states by a leader in the field.
- Heldmaier, G., and M. Klingenspor (eds.). 2000. *Life in the Cold*. Springer, New York. This is the symposium volume for the 11th International Hibernation Symposium.
- Heldmaier, G., S. Ortman, and R. Elvert. 2004. Natural hypometabolism during hibernation and daily torpor in mammals. *Respir. Physiol. Neurobiol.* 141: 317–329. A sweeping look at the phylogeny of mammalian hypothermic states, their adaptive significance, and the comparative physiology of hypometabolism.
- Heldmaier, G., and T. Ruf. 1992. Body temperature and metabolic rate during natural hypothermia in endotherms. *J. Comp. Physiol., B* 162: 696–706. Although becoming dated, an insightful treatment by two leaders in hibernation research. The paper by Heldmaier et al. 2004 follows up on themes raised in this paper.
- Nedergaard, J., and B. Cannon. 1990. Mammalian hibernation. *Philos. Trans. R. Soc. London B* 326: 669–686. Probably the most delightful, scientifically serious article ever written on hibernation.
- Ruf, T., and W. Arnold. 2008. Effects of polyunsaturated fatty acids on hibernation and torpor: a review and hypothesis. *Am. J. Physiol.* 294: R1044–R1052.
- Ruf, T., C. Bieber, W. Arnold, and E. Millesi (eds.). 2012. *Living in a Seasonal World: Thermoregulatory and Metabolic Adaptations*. Springer, New York. This is the symposium volume for the 14th International Hibernation Symposium.
- Stokkan, K.-A., B. E. H. van Oort, N. J. C. Tyler, and A. S. I. Loudon. 2007. Adaptations for life in the Arctic: evidence that melatonin rhythms in reindeer are not driven by a circadian oscillator but remain acutely sensitive to environmental photoperiod. *J. Pineal Res.* 43: 289–293.
- Turbill, C., C. Bieber, and T. Ruf. 2011. Hibernation is associated with increased survival and the evolution of slow life histories among mammals. *Proc. R. Soc. London, Ser. B* 278: 3355–3363.
- Vors, L. S., and M. S. Boyce. 2009. Global declines of caribou and reindeer. *Glob. Change Biol.* 15: 2626–2633.

See also **Additional References** and *Figure and Table Citations*.