The Company of Biologists

REVIEW

Adaptations to polar life in mammals and birds

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ABSTRACT

This Review presents a broad overview of adaptations of truly Arctic and Antarctic mammals and birds to the challenges of polar life. The polar environment may be characterized by grisly cold, scarcity of food and darkness in winter, and lush conditions and continuous light in summer. Resident animals cope with these changes by behavioural, physical and physiological means. These include responses aimed at reducing exposure, such as 'balling up', huddling and shelter building; seasonal changes in insulation by fur, plumage and blubber; and circulatory adjustments aimed at preservation of core temperature, to which end the periphery and extremities are cooled to increase insulation. Newborn altricial animals have profound tolerance to hypothermia, but depend on parental care for warmth, whereas precocial mammals are well insulated and respond to cold with non-shivering thermogenesis in brown adipose tissue, and precocial birds shiver to produce heat. Most polar animals prepare themselves for shortness of food during winter by the deposition of large amounts of fat in times of plenty during autumn. These deposits are governed by a sliding set-point for body fatness throughout winter so that they last until the sun reappears in spring. Polar animals are, like most others, primarily active during the light part of the day, but when the sun never sets in summer and darkness prevails during winter, high-latitude animals become intermittently active around the clock, allowing opportunistic feeding at all times. The importance of understanding the needs of the individuals of a species to understand the responses of populations in times of climate change is emphasized.

KEY WORDS: Arctic, Antarctic, Temperature regulation, Starvation, Photoperiod, Circadian rhythms

Introduction

The polar regions (the Arctic and Antarctic) are characterized by continuous light in the summer and almost total darkness, blizzards, scarcity of food and temperatures occasionally as low as −60°C in the winter. The Arctic is defined as the area north of the 10°C isotherm for July, whereas the Antarctic is the area south of the Antarctic Convergence (see Glossary); Arctic and Antarctic animals are those having their winter residency and main area of distribution within those boundaries (Box 1) (Irving, 1972; Blix, 2005). Probably because of the challenges imposed by this environment, the number of species that can cope with life in the polar regions is low, but most of those that prevail occur in large numbers. The effects of global warming are particularly felt in the polar regions, and an understanding of the needs of the animals therein and their tolerances to environmental change is greater than ever. This Review will focus primarily on the adaptations (see Glossary) of young and adults to low temperatures, and the effects of scarcity of food and lack of light during winter, as well as continuous light during summer, on animals that are permanent residents in polar regions.

Regulation of body temperature in polar animals
Maintaining core temperature in the cold

The ambient air temperature in the polar regions may persist at −40°C for extended periods, regularly reaching −50°C and occasionally even −60°C, whereas in the oceans, the temperatures are close to freezing. For a homeothermic animal exposed to these conditions, sometimes with a thermal gradient between the body core and the environment of almost 100°C, the challenge is first and foremost to balance heat loss against a minimal rate of metabolic heat production. In the polar regions, where, at least on land, energy is often in short supply, this is preferentially achieved by control of heat loss to the environment. There are three main avenues for heat loss – conduction/convection, radiation and evaporation – each of which must be controlled if the animal is to maintain a stable core temperature.

Defence of body temperature in the adult animal
Behavioural defences

The surface area of the animal over which heat is lost by conduction and radiation is in most cases considered constant, but this is not always true. In fact, many species, from polar bears (Øritsland, 1970) to redpolls (Brooks, 1978), can minimize their surface area to volume ratio by 'balling up' into a more or less spherical posture. This has the advantage that the surface over which heat is lost is reduced, while the heat-producing mass is the same, and the sphere is the form for which surface area in relation to volume is the smallest.

Animals living in colonies can also huddle to reduce heat loss. By standing or lying close together, the group's common mass is the same, while their common surface area is much smaller. However, with the exception of walruses during the moulting season (Fay and Rey, 1968), none of the adult Arctic mammals or birds are known to huddle, whereas emperor penguins in Antarctica do so extensively during severe weather (e.g. Le Maho, 1977; Ancel et al., 1997; Gilbert et al., 2006, 2007).

Animals can also reduce heat loss by constructing shelters in the ground or snow, or simply by curling up and allowing themselves to be snowed under. The construction of shelters is driven to perfection in the igloos of the Inuit, whereas simple burrows in the snow are used temporarily by polar bears (Blix and Lentfer, 1979), wolves (Mech, 1988), foxes (Prestrud, 1991, 1992), hares (Gray, 1993) and ptarmigan (Irving et al., 1967). Because of their small size, ermines and lemmings are thermally at such a disadvantage that they have to spend most of the winter in the subnivean space (see Glossary), where the temperature, depending on snow cover, may be stable at around 0°C (Coulianos and Johnels, 1962; Morrison, 1966; Korslund and Steen, 2006; Duchesne et al., 2011).

Physical defences

Polar birds and mammals protect themselves physically against the cold by growing a winter plumage and coat of fur,

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GLOSSARY

Ablation
Processes that remove snow, ice or water from a snowfield. The opposite of accumulation.

Adaptation
Term that differs among disciplines; here an evolutionary process by which an organism becomes fitted to its environment.

Altricial
Undeveloped and requiring parental care and nourishment.

Antarctic Convergence
A dynamic water-mass boundary, marked by sharp surface temperature gradients, that divides cold Antarctic waters from the more temperate water masses to the north.

Civil twilight
Morning civil twilight begins when the geometric centre of the sun is 6 deg below the horizon and ends at sunrise. Evening civil twilight begins at sunset and ends when the geometric centre of the sun reaches 6 deg below the horizon.

Guard hairs
The long coarse hairs forming a layer that covers and protects the soft wooly underfur.

Lanugo
A downy or wooly fetal covering of hair that in seals is retained for a short period after birth.

Lower critical temperature
Ambient temperature below which an animal has to increase its metabolic heat production to maintain deep body temperature.

Precocial
Capable of a high degree of independent activity from birth.

Rete
A structure consisting of a blood vessel that splits up into a great number of smaller vessels that run in parallel and eventually reunite into one vessel.

Subnivean
Under the snow.

Thermoneutral zone
The range of ambient temperatures over which an animal can maintain deep body temperature without increasing metabolic heat production.

Box 1. Animals of the Arctic and Antarctic

The terrestrial Arctic animals discussed in this Review are the polar bear (*Ursus maritimus*), polar wolf (*Canis lupus*), Arctic fox (*Vulpes lagopus*), ermine (*Mustela ermina*), muskox (*Ovibos moschatus*), reindeer/caribou (*Rangifer tarandus*), Arctic hare (*Lepus arcticus*) and lemming (*Dicrostonyx* sp./*Lemmus* sp.). The marine Arctic animals that are discussed are the bowhead whale (*Balaena mysticetus*), narwhal (*Monodon monoceros*), white whale (*Delphinapterus leucas*), bearded seal (*Erignatus barbatus*), ringed seal (*Pusa hispida*), hooded seal (*Cystophora cristata*), harp seal (*Pagophilus groenlandica*), ribbon seal (*Histriophoca fasciata*) and walrus (*Odobenus rosmarus*).

In the Antarctic there are no land mammals, but there are marine mammals, such as the crabeater seal (*Lobodon carcinophagus*), Ross seal (*Ommatophoca rossi*), Weddell seal (*Leptonychotes weddellii*) and leopard seal (*Hydrurga leptonyx*), which are closely associated with the pack ice.

The true Arctic birds are the snowy owl (*Nyctea scandiaca*), raven (*Corvus corax*), rock ptarmigan (*Lagopus mutus*) and Arctic redpoll (*Carduelis hornemanni*), as well as some little-known seabirds such as the ivory gull (*Pagophila eburnea*) and Ross gull (*Rhodo rosea*). In Antarctica, there are no resident terrestrial birds, but resident marine birds, such as Emperor (*Aptenodytes forsteri*) and Adélie (*Pygoscelis adeliaestethia*) penguins, Antarctic petrels (*Thalassoica antarctica*) and snow petrels (*Pagodroma nivea*), are abundant.

In addition, there are multitudes of migratory mammals and birds that visit the polar regions during summer. The Arctic ground squirrel (*Citellus parryi*) and the Djungarian (or Siberian) hamster (*Phodopus sungorus*), for example, are hibernators that are not normally considered as truly Arctic mammals (and hibernation is not a common Arctic strategy). However, the range of these animals extends into the Arctic, where they have been much studied (Heldmaier et al., 2004). They will therefore be considered, in brief, in this Review, and some studies of other sub-polar species with obvious relevance for the true polar species are included.

respectively, or by relying on a layer of blubber to prevent heat loss. The insulation properties of fur and plumage depend on the thermal conductivity of the individual hairs and feathers and their collective ability to trap a layer of air, which has only half the conductivity of most furs and plumages, next to the skin. The insulation value of the fur may be affected by both the density of hairs and their structure. In reindeer and caribou, for instance, each of the guard hairs (see Glossary) is hollow, containing thousands of air-filled cavities separated by thin septa (Timisjärvi et al., 1984; Blix et al., 2015).

The insulation provided by the fur of different animals varies significantly, and Scholander et al. (1950) have shown that the level of insulation increases with the thickness of the fur, which may be further enhanced by piloerection ('fluffing') of fur and plumage. The thickness and insulation value of fur and plumage of most polar animals change throughout the year. In muskoxen, all the under-wool, or qiviut, is shed in large sheets every spring and replenished in the autumn, whereas reindeer show similar, but less dramatic, changes (Mesteig et al., 2000), and the insulation by the plumage of ravens does not change at all (Schwan and Williams, 1978). The seasonal variations in fur are less notable in small mammals than in larger ones. The fur of ermine, for

instance, which has great value to man, has little value as insulation to the animal. Its thermal conductance is higher than that of other mammals of similar size, and although its colour changes seasonally, its thermal conductance does not (Casey and Casey, 1979; Brown and Lasiewski, 1972).

Clearly, the smallest animals are at a disadvantage in terms of their ability to use fur as an effective insulator, because they need to have short fur to be able to move. However, even in the largest of animals, the insulation value of the fur is influenced by a number of factors. The hairs of the polar bear, for instance, are very long and offer excellent insulation when dry, but polar bear fur loses almost all of its value when immersed in water (Scholander et al., 1950; Frisch et al., 1974), which conducts heat 25 times faster than air. The insulating properties of fur and plumage are also reduced by rain and sleet, and particularly by wind, which causes turbulence in the otherwise static layer of air between the feathers or hairs. For example, Gessaman (1972) found that wind exerted a strong cooling effect on adult snowy owls, causing their metabolic heat production to double in order to maintain body temperature even at a moderate wind speed of 7.5 m s^{-1} at −30°C. The effect of wind, however, has relatively minor effects on the heat loss from the largest animals, such as muskoxen and Svalbard reindeer, in which even gale force wind seems to cause little, if any, change in the insulation by the fur (Cuyler and Øritsland, 2002).

In seals, the fur has little insulative value, even when dry, and this is further reduced when wet (Frisch et al., 1974; Kvadsheim and Aarseth, 2002). Fur is missing entirely in whales; in these animals insulation is provided by a subcutaneous layer of blubber, which also acts as an energy store for times of food scarcity. Blubber generally provides much less insulation per unit depth than most

furs, but has the advantage of retaining its insulating properties in water (Kvadsheim et al., 1996; Kvadsheim and Folkow, 1997). The layer of blubber sometimes reaches enormous proportions, notably in bowhead whales, where it may be 30 cm thick! Like the fur of most polar terrestrial mammals, the blubber layer of polar seals also undergoes very marked seasonal changes (Nilssen et al., 1997; Lønø, 1970). Polar seal blubber reaches a low in summer, as a result of prolonged fasting during the moult, when the animal has to stay out of water to maintain the skin temperature necessary for regrowth of epidermal cells and fur (Feltz and Fay, 1966).

Adélie and emperor penguins are protected by a plumage that has exceptional insulation value in air, but this plumage is compressed during diving, and thereby loses much of its insulating effect. Although these birds have a layer of blubber, they are not thermally neutral in ice water (Kooyman et al., 1976).

Physiological defences

Heat loss by conduction may also be reduced by cooling the peripheral tissues while the core temperature is maintained. This is achieved by reducing peripheral and, in particular, cutaneous circulation, and can be visualized by means of infrared photography (Fig. 1A).

In both terrestrial and marine mammals and birds, the appendages represent relatively large surface areas that are less well insulated than the rest of the body, but excessive heat loss from them is prevented by special vascular arrangements that facilitate counter-current heat exchange. As early as 1955, Irving and Krog (1955) demonstrated that the feet of Arctic dogs, reindeer and seagulls may be at near-freezing temperatures while core body temperature is maintained at low ambient temperature. The anatomical arrangement of the heat exchangers that make this possible varies between species, but the general structure consists of arteries running in close contact with veins (Scholander and Schevill, 1955; Blix et al., 2010). The result is two concentric conduits, where the warm arterial blood is cooled by the venous blood, which has been chilled in the legs or flippers. The blood supply to the legs and flippers can also be routed through the great superficial veins. In animals such as reindeer, the legs are so long that effective heat exchange simply occurs between the brachial/femoral artery and vein, whereas in seals the flippers are so short that the heat exchanger has been made more effective by the vein being split up into numerous vessels running in parallel around the artery. Effective vasomotor control allows variation in the distribution of blood flow between these pathways, so that the extremities can function to dissipate or conserve heat, depending on the heat load on the animal (Fig. 1B). In Arctic wolves and foxes, foot temperature is maintained near 0°C by a cutaneous vascular plexus in their paw and toe pads, which allows the foot skin temperature to be regulated to within a degree of freezing, even when animals are standing on substrates of −50°C (Henshaw et al., 1972). A similar vascular arrangement is also found in sea birds (e.g. Midtgård, 1981; Midtgård and Bech, 1981; Johansen and Bech, 1983), and Johansen (1969) has shown that peripheral arteries of a variety of Arctic seals are responsive to sympathetic stimulation almost down to freezing. This begs the question of how the peripheral nerves and the vascular smooth muscles can operate to attain this degree of sensory and vascular control at such temperatures. Miller (1965) has shown that conduction velocity of peripheral nerves from a variety of Arctic animals is much reduced at very low temperatures, but they are still able to conduct, even when supercooled to −6°C. However, Miller and Irving (1967) demonstrated that this is also the case in temperate zone muskrats (*Ondatra zibethicus*), so this seems to apply to all
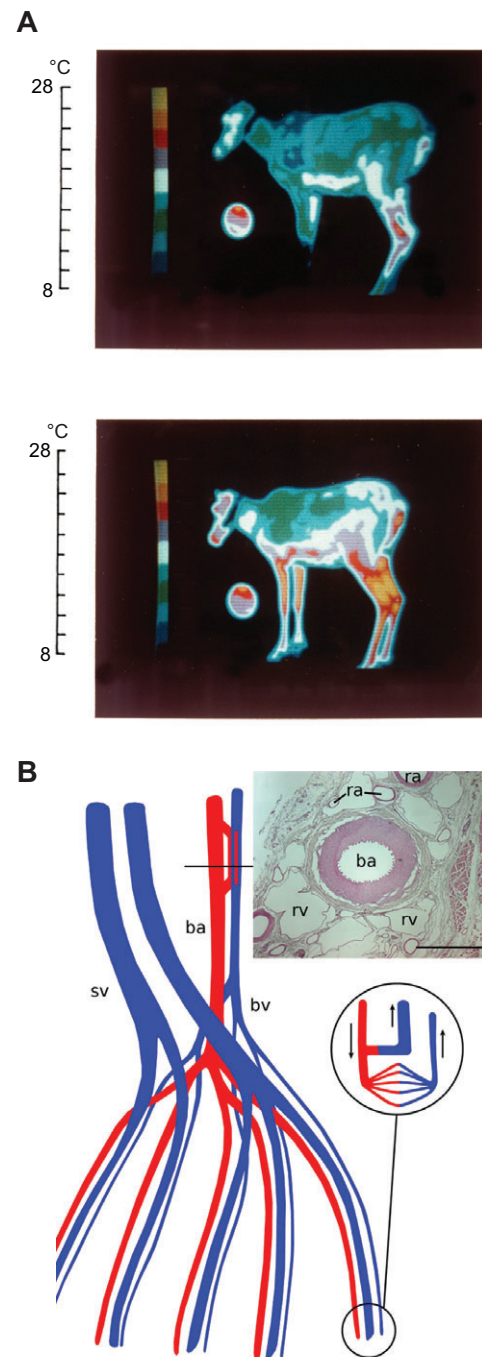
Fig. 1. Limiting heat loss by peripheral vasoconstriction. (A) A reindeer pictured by infra-red photography before (top) and immediately after (bottom) a 45-min period of running at 9 km h^{-1} on a level treadmill at an ambient temperature of 2°C in summer. The surface-temperature colour scale relates to the temperature (°C) scale to the left. The circular figure (in front of animal) is a black body that was heated separately and used as temperature reference. Adapted from Johnsen et al. (1985b). (B) A simplified diagram of the fore-flipper circulation in a hooded seal (left), showing the central brachial artery (red; ba) and vein (blue; bv) and the great superficial veins (sv). Inset top right: a light microscopical cross-section through the counter-current heat exchanger at the base of the flipper. The prominent brachial artery (ba) is in the centre, with several rete arteries (ra) and numerous rete veins (rv) surrounding the brachial artery. The great superficial veins are outside the field of vision in this section. Scale bar: 1 mm. Inset centre right: the two alternative routes for arterial blood in the flipper: through capillaries, for tissue nutrition, to the heat exchanger for heat conservation, or through arterio-venous shunts to the superficial veins for body cooling. Arrows show direction of blood flow. Adapted from Blix et al. (2010).

nerves of uninsulated extremities that are regularly exposed to cold. Meng et al. (1969), moreover, found that the fatty acid composition of caribou leg bone marrow decreased in saturation and melting point distally, and Brix and colleagues have demonstrated in a series of papers (e.g. Brix et al., 1990) that the haemoglobin of reindeer and muskoxen have properties that safeguard oxygen unloading at low temperatures (e.g. a very low enthalpy change for the reaction with oxygen).

In addition, Arctic mammals and birds protect themselves from the cold by restricting evaporative heat and water loss from the respiratory tract. The basis for nasal heat and water conservation is, again, counter-current heat exchange in the nasal mucosa (Jackson and Schmidt-Nielsen, 1964). In reindeer, the nasal cavities are filled with an elaborate system of scrolled structures, called concae (Fig. 2A), which are coated with a richly vascularized mucosal layer. The concae both increase the surface area over which heat exchange can occur and divide the airflow into thin layers. Cold inhaled air passes over the warmer mucosa and, as a result, is heated to body temperature and saturated with water vapour before reaching the lungs. The nasal mucosa, in which the blood in an arterial and a venous rete (see Glossary) is running counter-current, is thereby cooled and stays cool while the (warm) air stays in the lungs. When the animal exhales, the warm humid air passes down a temperature gradient as it flows over the cold mucosa and is cooled, and the water vapour therefore condenses. The result is that the animal exhales cold and 'dry' air; thus, heat and water are saved (Fig. 2C). The nasal cavities of other Arctic terrestrial mammals are organized similarly to those of reindeer, whereas seals have arrived at a different solution. Here, the nasal surfaces have developed into a highly convoluted mass, reminiscent of a car radiator, with an air space of <1 mm between the lamellae (Folkow et al., 1988). This structure allows ∼65% of the heat and ∼80% of the water added to the inspired air to be regained on expiration at an ambient temperature of −25°C in both reindeer and seals (Blix and Johnsen, 1983; Folkow and Blix, 1987, 1989).

However, nasal heat exchange is not simply a passive process in reindeer. Blix and Johnsen (1983) found that, at any given ambient temperature, the temperature of air expired by the reindeer is consistently lower in summer (when fur insulation is low) than in winter (when it is high). This implies that the animal is capable of adjusting the efficiency of the nasal heat exchange to maintain thermal balance along with the great seasonal changes in body insulation (Fig. 2B) (see Johnsen et al., 1985a,b; Mercer et al., 1985).

Metabolic rate and energy expenditure

The mechanisms discussed above extend the thermoneutral zone (see Glossary) in which the animal can exist on a minimal resting metabolic rate (RMR) and thereby minimize energy expenditure. However, when the lower critical temperature (see Glossary) of the individual has been reached, RMR increases linearly with decreasing ambient temperature (Fig. 3). This increase in metabolic rate is achieved by shivering (e.g. Aulie, 1976) (or physical activity) in mammals and birds, or non-shivering thermogenesis in brown adipose tissue (BAT; see Box 2) in mammals. The lower critical temperature and the total conductance of the animal, as determined in the laboratory, is a good indication of the thermal adaptation of the species, but cannot be taken as a measure of when the wild animal will reach its thermal limits. Wind and precipitation may drastically increase the conductance of the animal, and Øritsland and Ronald (1973), by contrast, have shown that solar radiation may significantly contribute to warming in harp
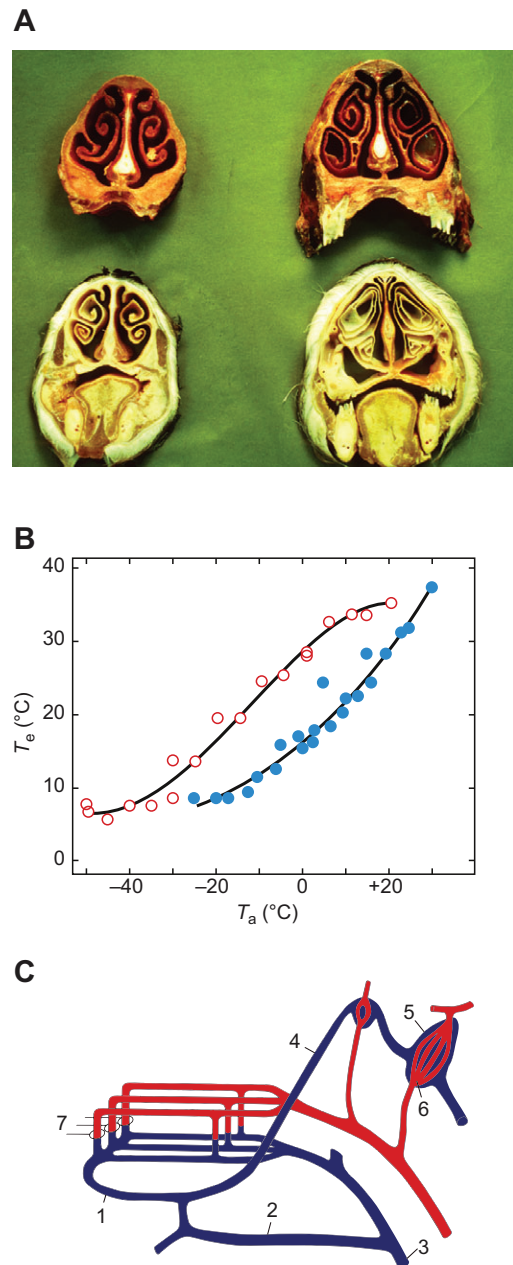
Fig. 2. Restricting evaporative heat and water loss in the cold and selective brain cooling when warm, by nasal heat exchange. (A) Cross-sections through the nose of muskoxen (top) and reindeer (bottom) at the tip of the nose (left) and at the base (right) reveal the structure of the concae. (B) Exhaled air temperature (T_e) in summer (filled blue symbols) and in winter (open red symbols) at different ambient temperatures (T_a) in reindeer. Adapted from Blix and Johnsen (1983). (C) A simplified diagram of arterial and venous vasculature of the left side of a reindeer head. Arteries are shown in red and veins are shown in blue. During heat conservation in the cold, blood runs counter-current in the retia of the nasal mucosa (left) and leaves through the sphenopalatine group of veins for the jugular vein (3), with the dorsal nasal vein (1) constricted. The efficiency of the nasal heat and water exchange will depend on blood flow to the nasal mucosa, the number of open arterio-venous shunts (7) and respiratory frequency. During extreme heat stress, blood flow in the nasal mucosa is in the caudal direction, as the shunts (7) are open and the facial veins (2) are constricted. Thus, the now cold venous effluent from the nasal mucosa is routed to the cavernous sinus (5) through the now dilated angular oculi vein (4). Heat is then exchanged between the cold blood in the sinus and warm blood in a rete of the carotid artery (6) on its way to the brain. Adapted from Johnsen et al. (1985a), Johnsen and Folkow (1988) and Blix et al. (2011).
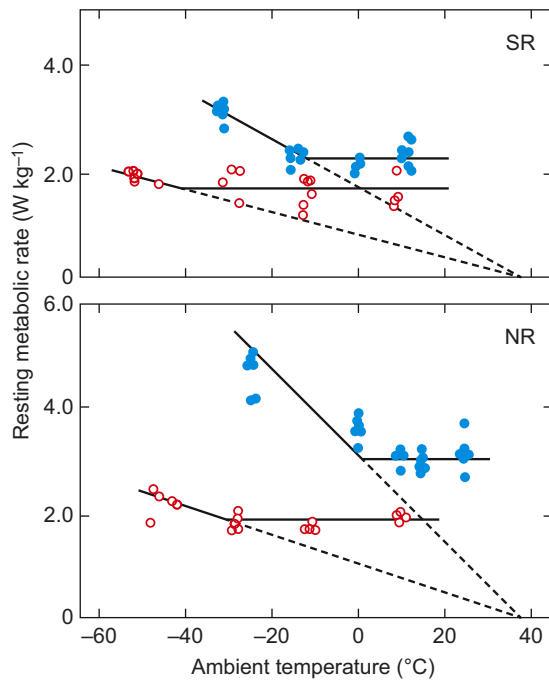
Fig. 3. Metabolic responses to cold in reindeer. Resting metabolic rate at different ambient temperatures in summer (filled blue symbols) and winter (open red symbols) in adult Svalbard (SR) and mainland Norwegian (NR) reindeer. The animals show a resting metabolic rate of 2.0 W kg^{-1} in the thermoneutral zone, with a lower critical temperature of −30°C in NR reindeer during winter. The slope of the line reflects the total conductance of the animal. Dashed lines are extrapolations to body temperature. Body temperature is 38.6°C. Adapted from Nilssen et al. (1984a).

seals. It is white hairs, in particular, that transmit much of the visible and near-infra-red radiation through the pelt, to be absorbed in the dark skin. Contrary to popular belief (Mirsky, 1988), UV light contributes little, if anything, to thermoregulation in polar bears or any other polar animal.

Box 2. Brown adipose tissue and non-shivering thermogenesis
Brown adipose tissue (BAT) is microscopically characterized by cells with large nuclei, many small fat droplets and a multitude of dense mitochondria. BAT produces heat in response to cold. It is activated by noradrenaline either released from nerve endings in the tissue itself or reaching the tissue via the blood. Noradrenaline initiates triglyceride breakdown, primarily via β$_3$-adrenergic receptors, cAMP and protein kinase A, leading to release of free fatty acids (FFAs) that are both the substrate for non-shivering thermogenesis and the regulators of the activity of uncoupling protein-1 (UCP1, thermogenin). The combustion of FFAs leads to extrusion of H$^+$, and UCP1 thus allows for mitochondrial combustion of FFAs that is uncoupled from the production of ATP; instead, the energy is released as heat. For more detail, see Cannon and Nedergaard (2004). The amount of BAT in newborn Arctic animals can be very large (Fig. 4B) and its contribution to the total metabolic capacity can amount to 60–70% of summit metabolism in newborn reindeer (Markussen et al., 1985). BAT atrophies when no longer needed, and it was long assumed to be active only in neonates and small animals. However, it was recently discovered that defined regions of functionally active BAT are present in adult humans (e.g. Cypess et al., 2009) and it is assumed that this tissue is important for body mass regulation, at least in humans (e.g. Virtanen et al., 2009).

The Svalbard reindeer is so well insulated that although its lower critical temperature in winter is as low as −40°C, its RMR is still only marginally increased at −50°C (Fig. 3). It is conspicuous that the RMR of these animals appears to be much reduced in winter compared with summer. Nilssen and colleagues have shown, however, that this is the result of a much reduced food intake during winter, whereas fasting metabolic rate is the same in both seasons (Nilssen et al., 1984a).

Preventing overheating
In animals that are insulated to withstand extremely cold conditions and with few avenues for heat loss, physical activity poses a potentially serious risk of overheating. Reindeer (Aas-Hansen et al., 2000) and most other terrestrial animals are capable of panting and peripheral vasodilatation (Fig. 1A), but during periods of physical exertion in winter, reindeer can easily become overheated. In such cases, the animal may resort to selective brain cooling. This is based on the delivery of cold blood from the nasal mucosa via the angular ocular vein to a cavernous venous sinus at the base of the brain. Here, heat is exchanged with warm blood in the carotid artery, into which a rete is inserted to facilitate heat transfer. The result of this is that the brain is cooled selectively while heat is stored (as increased temperature) in the rest of the body to be dissipated when the stress has passed (Fig. 2C) (see Johnsen et al., 1987; Johnsen and Folkow, 1988; Blix et al., 2011).

The polar bear does not have any brain cooling mechanisms, and risks overheating on the rare occasions when it runs, owing to the animal's heavy legs and paws and the sideways motion of the gait (Hurst et al., 1982). Fortunately, bears, seals and penguins can, in most cases, prevent overheating by jumping into ice water. Whales are even more fortunate when it comes to the thermal consequences of locomotion. Any additional heat load that is caused by swimming can effectively be lost into the cold oceans by cutaneous vasodilatation (Folkow and Blix, 1992), and the cost of swimming, and hence, daily energy expenditure, in whales is remarkably low (Blix and Folkow, 1995).

Thermoregulation in young animals
Different polar species give birth at different times under various thermal conditions, but all offspring have in common a much larger exposed surface area relative to body mass than the adults. They also have less insulation, particularly when wet immediately following birth or hatching. The offspring of both mammals and birds can roughly be classified as either precocial or altricial (see Glossary). As for adult animals, thermoregulation in offspring can involve behavioural, physical and physiological mechanisms (e.g. Blix and Steen, 1979; Blix, 2005).

Altricial young
Altricial young are born or hatched in an undeveloped state, and mammals and birds with altricial offspring usually produce a litter of young in a den, cave or nest (Blix and Steen, 1979). The polar bear and the lemming are typical examples. Polar bears give birth to cubs that only weigh 600–800 g, whereas newborn lemmings weigh in at only 5 g. At first, both depend heavily on maternal care and the shelter provided by the den or nest. However, although the bears never leave their cubs until they vacate the den after 3 months (Blix and Lentfer, 1979), the lemming pups are occasionally left alone when the mother goes out to feed. During such episodes, the most important survival factor in these, and many other altricial young (Blix and Steen, 1979), is profound tolerance to hypothermia (Østbye, 1965) (Fig. 4A). As the offspring grow, they show a progressively increasing ability

A

B
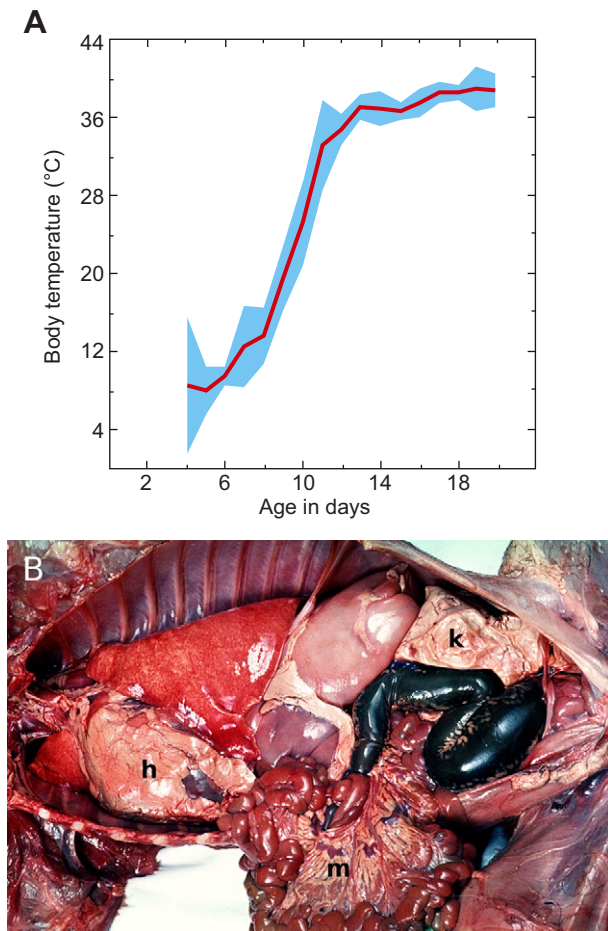
Fig. 4. Cold defence in the newborn. (A) Altricial young show extreme tolerance to hypothermia. Body temperatures of lemmings of different ages (red line) after a 30-min exposure to air temperatures of 2°C are shown. Blue shading, s.e.m. No ill effects were observed when the pups subsequently were delivered back to the mother in the nest. Adapted from Østbye (1965). (B) Precocial newborn muskoxen show massive deposits of brown adipose tissue around the heart (h), kidneys (k) and mesentery (m). Photo credit: A. S. Blix.

to thermoregulate, caused by increased ability to shiver, and improved insulation, greater size and, in some cases, development of thermogenic BAT (Morrison et al., 1954; Hissa, 1964; Christiansen, 1977; Blix and Lentfer, 1979).

Parental heat and the protection of a nest are also important means of maintaining body temperature in young altricial birds in the Arctic (Blix and Steen, 1979). In the Antarctic, the Antarctic petrel and some of the snow petrels breed on exposed nunataks without the benefit of a nest, sometimes at ambient temperatures of −25°C. These chicks depend on constant parental brooding until 11 days of age (Bech et al., 1991).

Of course, the behaviour of the offspring themselves also has a role in their thermoregulation. Young, thermally dependent mammals or birds usually huddle together on occasions when they are left alone, as do abandoned young emperor penguins when the weather becomes severe (Le Maho, 1977).

Precocial young

Precocial young are born or hatched with well-developed physical and physiological defences against the cold. The ptarmigan chick and reindeer and muskoxen calves are typical examples. The ptarmigan chicks hatch with an effective down plumage and are able to travel large distances even on their first day, and they have a substantial thermogenic capacity, which is based primarily on shivering in their breast muscle (Aulie and Steen, 1976). Even so, the chicks have to return to the mother for brooding when their body temperature approaches 35°C (Theberge and West, 1973); they apparently use their thermogenic capacity only to restrict their cooling rate so that the duration of their feeding excursions becomes less dependent on ambient temperature (Jørgensen and Blix, 1988).

Muskoxen and reindeer give birth in early spring when the climatic conditions in the Arctic may be severe and the ground still covered with snow (Blix and Steen, 1979). At birth, the reindeer calves are well insulated by a pelt of air-filled hairs, and the muskox calves are equipped with a pelt of qiviut wool of very high insulation value. However, unlike those of the adults, these pelts lose much of their insulation value when exposed to wind or, even worse, to a combination of wind and rain or sleet (Lentz and Hart, 1960; Blix et al., 1984; Markussen et al., 1985). In newborn reindeer (Markussen et al., 1985; Soppela et al., 1986, 1992), and even more so in muskox calves (Fig. 4B; Blix et al., 1984), deposits of highly thermogenic BAT are the major source of heat. In reindeer, these deposits may contribute as much as 60–70% to peak metabolism (Markussen et al., 1985).

Arctic hare leverets are intermediate between altricial and precocial. After a few days of intensive nursing (Aniskowicz et al., 1990), the leverets are able to fend for themselves in between periodic nursing. It is most likely that these animals, like other lagomorphs (Hull and Segall, 1965), are also equipped with BAT at birth.

Most polar seal species give birth on open ice floes during early spring; at the moment of birth, the pups have to take the full brunt of the harsh climate and survive exposure to a thermogradient that may exceed 60°C, often in combination with strong winds (e.g. Blix and Steen, 1979). The one exception is the Arctic ringed seal, which gives birth in a snow lair on the shore-fast ice (Smith et al., 1991). The size and insulation of the newborn pups are amazingly varied in the Arctic. Most polar seals are born with a lanugo fur (see Glossary), an exception being the hooded seal pup (Blix and Steen, 1979). Lanugo pelts offer good insulation value as long as they stay dry, but not when wet (Kvadsheim and Aarseth, 2002). When exposed to solar radiation, these pelts may contribute to the heating of the animal (Øritsland and Ronald, 1973).

The small newborn pups of the ringed seals, the harp seals and probably the little-known ribbon seals, are equipped with very large amounts of highly thermogenic BAT, which is their main defence against the cold at the moment of birth and when the weather turns severe (Blix et al., 1979). The larger newborns of hooded seals, bearded seals and walrus do not have functional BAT (Blix and Steen, 1979). However, the skeletal muscles of the northern fur seal (*Callorhinus ursinus*) may be engaged in non-shivering thermogenesis when the pups are exposed to cold (Grav and Blix, 1979). Unfortunately, it is not known whether this form of heat production is active in polar seals, or in a likely candidate, the emperor penguin, which, like other birds (e.g. Johnston, 1971; Saarela et al., 1991), does not have any BAT.

Although ringed seals, bearded seals and walruses are semi-aquatic shortly after birth (e.g. Lydersen and Hammill, 1993), Arctic whales are, of course, truly aquatic from the very moment of birth. Newborn Arctic whales are equipped with a relatively thin layer of blubber (Mansfield et al., 1975), and, like some of the seals, benefit from their large body mass, which in the newborn bowhead whale is about a ton!

Milk

The energy required to support the high metabolism in both altricial and precocial newborn polar mammals is obtained from the

mother's milk. The milk produced by polar marine mammals has a fat content of 40–50% (e.g. Kooyman and Drabek, 1968; Lauer and Baker, 1969; Debier et al., 1999). The nursing period varies greatly, from a world-record minimum of 2–4 days in the hooded seal (Bowen et al., 1985) to more than a year in the walrus. Terrestrial polar species have milk with a fat content of 10–20% (e.g. Baker et al., 1970, Cook et al., 1970; Luick et al., 1974), whereas the milk of cows and humans has a fat content of only ~4%.

Coping with variations in food availability

As well as withstanding the seasonal changes in ambient temperature, polar animals have to cope with the even more remarkable seasonal changes in both availability and energy density of their food. This is particularly challenging on the high Arctic archipelago of Svalbard. Here, because of the effect of the warm Atlantic current, the climate, particularly on the western coasts, is unusually warm in mid-winter – there can even be episodic rain. When such warm spells are followed by periods of low temperatures, the result is over-icing of the range and a marked reduction in the availability of plant material, which has a rather low energy density to begin with during winter. Furthermore, there is a significant additional energy cost of digging through the hard snow and ice (Fancy and White, 1985b).

Metabolic and behavioural responses

Some Arctic animals are able to save energy by reductions in basal metabolic rate in winter. For example, muskoxen show a 30% reduction (Nilssen et al., 1994), and a reduced winter metabolic rate has also been reported in Arctic hare (Wang et al., 1973), Arctic fox (Fuglesteg et al., 2006) and rock ptarmigan (Mortensen and Blix, 1986); this will be of great significance to the animal when food is in short supply.

When food supply is limited, energy expenditure can also be limited by reducing total daily physical activity. The daily energy cost of locomotion is influenced by three variables: the total distance travelled, the distance climbed and the nature of the surface over which the animal travels. Reindeer expend 30% more energy when walking on wet tundra compared with on hard-packed roads (White and Yousef, 1978; Fancy and White, 1985a), and the cost of walking across soft or crusted snow is even higher. A Svalbard reindeer, may, owing to the lack of predators, spend 80% of its day lying down or standing and <2% walking and trotting in winter (Tyler, 1987). This is energetically very advantageous, because even a moderate trotting speed of 7 km h^{-1} increases energy expenditure four times on solid ground in treadmill experiments (Nilssen et al., 1984b).

Fat storage

Most polar animals prepare themselves for periods of reduced food availability by deposition of body fat during times of plenty in summer and early autumn (Fig. 5). The Svalbard rock ptarmigan has been much studied in this respect. These birds start to deposit fat in August when there is no longer midnight sun, and they reach their peak levels of fat storage in late November when there is no longer any light. At their peak, fat stores account for 30% of the animals' total body mass. However, all the fat has disappeared by February, when daylight reappears on the islands (Mortensen et al., 1983). Moreover, these changes also happen when captive birds are fed *ad libitum* throughout the year (Stokkan et al., 1986). The fat reserves are therefore not, as previously thought, used to supplement the daily energy budget during winter, but are instead carefully kept in store for episodes of acute starvation during winter storms (Mortensen and Blix, 1985). It follows that the ptarmigans [and Arctic foxes (Fuglesteg et al., 2006)] seem to reduce their fat
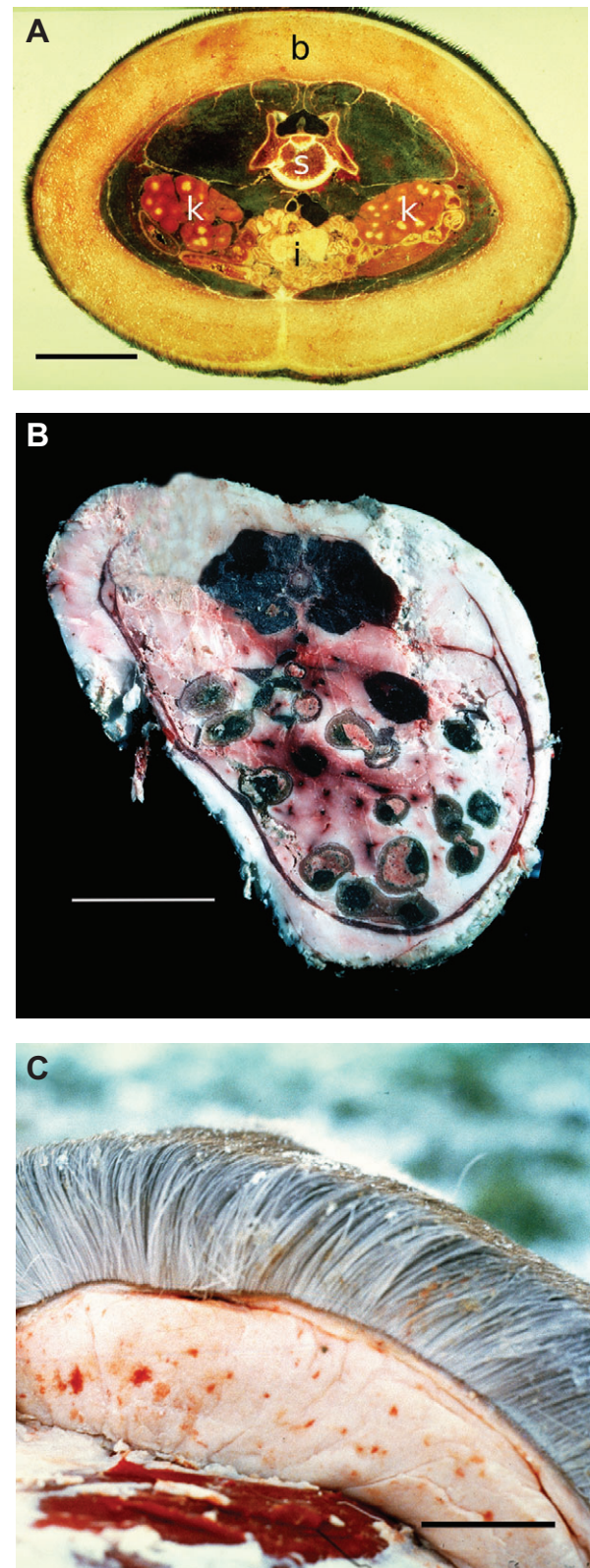
Fig. 5. Fat storage in Arctic animals in winter. (A) A cross-section through a harp seal, at the level of the umbilicus. b, blubber; k, kidneys; i, intestines; s, spine. Photo credit: E. S. Nordøy. (B) A cross-section through the abdomen of a frozen carcass of an Arctic fox in winter. The spine and lumbar muscles are visible in the upper part, and intestines are visible in the lower part. The carcass was partly squeezed during freezing. Photo credit: P. Prestrud. (C) The subcutaneous rump fat in Svalbard reindeer in autumn. Photo credit: K. Bye. Scale bars in all panels: 5 cm.

reserves according to a seasonally changing set-point for body mass, as the chance of death by starvation steadily diminishes with the return of light (Mortensen and Blix, 1986). This is also observed in Svalbard reindeer (Larsen et al., 1985; Tyler, 1987). The fat reserves (Fig. 5C) in reindeer are important not only for the survival of the individual, but also for reproduction of the species. For instance, fertility and conception in the high Arctic Peary caribou is dependent on a certain body mass and fat content, to the extent that a difference in body mass of only 7% increases the pregnancy rate from 8% to 90% (Thomas, 1982). A similar relationship is found in muskoxen (Adamczewski et al., 1998).

The metabolic role of white fat is complex, and it is now clear that this tissue is a major secretory and endocrine organ. Leptin, for example, is a hormone, produced primarily by white fat, that is crucial for energy balance, and there is a correlation between plasma leptin and indices of body fatness in both human subjects and some experimental animals (e.g. Trayhurn and Beattie, 2001). In very seasonal animals, such as the Arctic fox, plasma leptin does not react to food deprivation (Fuglei et al., 2004), whereas plasma leptin decreases when reindeer receive a fat- and protein-depleted diet (Soppela et al., 2008). It follows that there is still much to be learned about this hormone in high-latitude animals.

Hibernation and starvation

It is common knowledge that bears enter dens in the late autumn and hibernate over winter to save energy when food is in short supply. In the case of polar bears, however, it is only the pregnant females that overwinter in dens; sub-adults and males remain, more or less, active throughout the year. In preparation for this sojourn, the females may accumulate as much as 40% of body mass as fat (Lønø, 1970; Atkinson and Ramsay, 1995). While in the den, they do not eat, urinate or defecate, and they preserve protein by recycling urea, while fat is combusted for energy (Nelson et al., 1973; Ramsay et al., 1991). Even though male polar bears do not spend extended periods in a den, they nevertheless accumulate large amounts of fat in preparation for periods of fasting, which, in some areas, may last for 7 months during the open-water season (Atkinson et al., 1996; Robbins et al., 2012).

Unlike small hibernators, such as the Arctic ground squirrel, that can cool to sub-zero temperatures and become torpid during hibernation bouts (e.g. Barnes, 1989), the body temperature of hibernating bears is only reduced by 6°C, while metabolic rate is reduced to only 25% of the normal rate (Toien et al., 2011). This is possible because of the large fat reserves, effective insulation and, in particular, the large body mass of these animals. Moreover, unlike small hibernators, bears do not suffer significant bone loss during hibernation (Lennox and Goodship, 2008), and they do not show the costly periodical arousals to normothermia (Heldmaier et al., 2004). Another special case is the Djungarian hamster. These animals only weigh ~30 g and undergo torpor only for a few hours during the day; in this way they may reduce their daily energy expenses by ~70%, although body core temperature is only reduced to ~20°C (Heldmaier et al., 2004).

A final example of episodic starvation in the polar regions is the fasting of both neonate and adult seals during moulting, when metabolic rate is reduced by ~50%, and 96% of their energy expenditure is covered by combustion of fat (Fig. 5A), whereas only 4% is derived from catabolism of protein (Nordøy et al., 1990). This strategy is so effective that the pups can cope with a fast, without access to water, of 52 days duration (Nordøy et al., 1992). Similar phenomena have been observed in both emperor and king penguins (Cherel et al., 1987; Robin et al., 1988; Groscolas, 1990).

Hoarding behaviour

Arctic foxes have two ways of storing energy: firstly, by the usual deposition of fat, and secondly, by surplus killing and subsequent hoarding of food during summer (Prestrud, 1991). The fat reserves are, as usual, deposited in September–October, and reach a maximum in November–March, after which they drop to very low levels in June. However, although some foxes may show a record fatness of 40% of body mass during winter (Fig. 5B), some do not possess visible fat reserves at all, reflecting the fact that fat reserves are regulated less by physiological means than by the sometimes wide variation in food supply (Prestrud and Nilssen, 1992). Foxes employ both 'scatter hoarding' (hiding single items of prey at dispersed sites) and 'larder hoarding' (hiding many prey items near the den site). Most of the hoarding is associated with superabundance of prey, such as in the vicinity of bird-cliffs – the largest documented Arctic fox larder contained no less than 136 sea birds (Sklepkovych and Montevecchi, 1996). Such hoarding is also normal for ermines, which have been found to hoard 150 lemmings in one of several deposits (Johnsen, 1969).

The Arctic redpoll is also known to store food, albeit in a different manner to the Arctic fox or ermine. This bird only weighs 12–15 g and survives at temperatures of −40°C for prolonged periods. The Arctic redpoll obviously operates precariously near the edge, but survives winter by a combination of increased metabolic capacity in the daytime and reduced metabolic rate during the night – in extreme situations with reduced body temperature – when resting in a sheltered location and digesting seeds that were stored in huge oesophageal diverticula during the day (Irving, 1972; Brooks, 1978).

Variations in photoperiod

The polar regions are, more than anything else, typified by long continuous nights in winter and long continuous days in summer. During the periods of alternating day and night between the periods of constant darkness and midnight sun, the length of the day may change by more than 30 min per day in places such as Svalbard, northern Greenland and Canada. These unusual aspects of the photoperiod are probably the only unique features of the polar regions, and the adaptations to them are the only ones that make polar biology truly special. It is the photoperiod that gives the polar animals both their clock and their calendar, and a number of reviews have recently outlined our current understanding of how this is achieved (Bloch et al., 2013; Hut et al., 2013; Gwinner and Brandstätter, 2001; Hazlerigg and Simonneaux, 2015; Steiger et al., 2013; Williams et al., 2015). Briefly, information on lighting conditions is received through the eyes and transmitted to the pineal gland, which, in the absence of light, will produce the hormone melatonin. This hormone synchronizes the inherent daily, or circadian, rhythms of the body. The basic mechanisms behind the regulation of seasonal or circannual events, such as reproduction and moult, are more complex and less well understood (Hazlerigg and Simonneaux, 2015), and are beyond the scope of this Review. It may be that melatonin signals associated with equinoxes directly entrain a circannual clock (Lincoln et al., 2003, 2006; Lu et al., 2010; Hazlerigg and Lincoln, 2011; Williams et al., 2015).

West (1968) found that ptarmigans at Fairbanks, Alaska, started their feeding activity at the beginning of morning civil twilight (see Glossary) and became inactive in the evening when civil twilight ended, and that a major part of their activity took place during the periods of civil twilight. Most animals are active during the light part of the day and rest during night; this raises several questions with regard to how animals at very high latitudes, where the sun

never sets during summer (and never rises during the winter), gain sufficient photoperiodic information to synchronize their clocks and, thereby, their daily activity. Apparently this differs between species. Krüll (1976a,b) found that snow buntings (*Plectrophenax nivalis*) that were transported from Germany to Svalbard during summer were active during what would have been the day and rested during what would have been night in Germany, suggesting that these birds were able to synchronize their activity based on the changes in the spectral composition of the light during the continuous day. This was later confirmed by Pohl (1999) in the common redpoll (*Carduelis f. flammea*). However, this is not the case in humans, who instead display free-running rhythmicity with a period of ~26 h under continuous light conditions at Svalbard (Johnsson et al., 1979). What about the animals that reside at high latitudes throughout the year? Stokkan and colleagues (Stokkan et al., 1986) studied the resident high Arctic rock ptarmigan at 79°N in Svalbard throughout the year. They found that, like other animals, this bird showed a diel feeding rhythm – feeding primarily in the morning and evening – when there was a difference between day and night during spring and autumn. However, during the continuous polar night, as well as during the continuous polar day, their feeding activity was intermittently continuous around the clock (Fig. 6) (Stokkan et al., 1986). In summer (the only time that was investigated), the activity pattern of the Adélie penguins in Antarctica has since been shown to be similar to that of the Svalbard ptarmigan (Wilson et al., 1989). The same pattern has also been confirmed in the Svalbard reindeer (Van Oort et al., 2005, 2007).

In the Antarctic, it is only the male emperor penguin that experiences complete darkness during winter, as the females are off to feed at sea, and these birds do not eat or move during this time, as they are incubating eggs (Le Maho, 1977). These animals do not show any 'nocturnal' peak in melatonin, during either Antarctic summer or winter (Miché et al., 1991). This is also the case for reindeer (Stokkan et al., 1994; Eloranta et al., 1995) and, during the Antarctic summer, the Adélie penguin (Cockrem, 1991) and the Weddell seal (Barrell and Montgomery, 1989). This independence of strong circadian constraints during summer and winter allows opportunistic feeding behaviour, which may make an important difference for animals constantly living on the edge. In reindeer, this may be further facilitated in winter by the apparent extension of their visual range into the ultraviolet (Hogg et al., 2011); it is surmised that this may enhance their ability to discriminate plants in snow (Tyler et al., 2014).

Polar animals in a warmer world

It is well established that climate warming is occurring in the Arctic at twice the global average rate [e.g. Arctic Climate Impact Assessment (ACIA), 2005], and the biota of the Arctic are thought to be particularly sensitive to the direct and indirect consequences of climate change (ACIA, 2005; Post et al., 2009). However, the situation in Antarctica is less clear. It is beyond the scope of this Review to speculate on the multitudes of possible effects of climate warming in the polar regions, but until now it has been the prerogative of ecologists to provide the scientific input to the ongoing debate about effects of climate change. Their focus is on populations, which is important, but it should be emphasized that populations consist of individuals with their specific needs and tolerances to change, and that, ultimately, it is the survival of the individuals that determines the fate of the population. Thus, more emphasis on experimental biology is called for in order to understand the effects of climate change on different species. Three examples, among many, that are conspicuous and causing
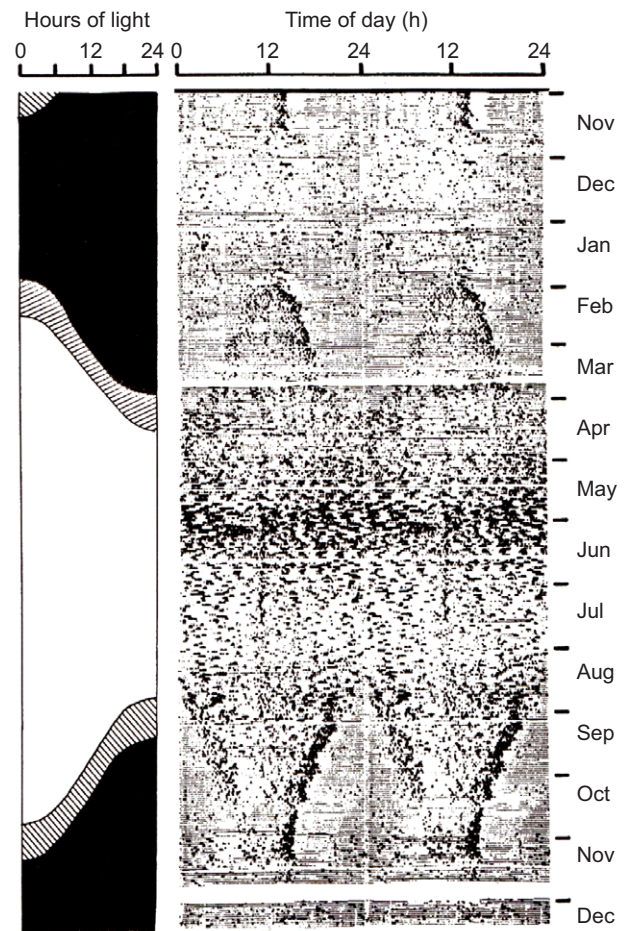
Fig. 6. Feeding patterns of Svalbard ptarmigan throughout the year. Left: annual variation in day length at Ny-Ålesund (79°N), Svalbard (darkness is indicated by black, civil twilight by hatching and light by white). Right: the feeding rhythm of Svalbard ptarmigan fed *ad libitum* under natural temperature and light conditions at Ny-Ålesund throughout a year. Each point represents a feeding event. Note that the graph has been duplicated to facilitate identification of the feeding rhythms. Reprinted from Stokkan et al. (1986).

concern may illustrate this point and are discussed briefly below: (1) the diminishing volume and reduced summer extension of the perennial sea ice in the Arctic Ocean (e.g. Tilling et al., 2015), (2) changes in the conditions of the subnivean space (Kausrud et al., 2008) and (3) mismatch between light- and temperature-driven responses (Post et al., 2009; Zimova et al., 2014).

Polar bears depend on hunting seals on the sea ice, and because the sea ice is breaking up at progressively earlier dates, the bears must endure longer fasts during the open-water period. This will likely cause increased mortality among bears (Hunter et al., 2010; Robbins et al., 2012) and increased predation of land-based alternative prey (Smith et al., 2010). Moreover, more bears will be exposed to ice water, and experimental work has shown that the likelihood of more juvenile bears freezing to death will increase (Blix and Lentfer, 1979).

Winter conditions are likely to be critical for the survival of small high-latitude rodents, and reductions in the condition and/or duration of their subnivean habitat are likely to affect the rodent community through temperature stress, flooding risk, food limitation and even predator access (Kausrud et al., 2008). This is supported by experimental evidence that extension of the available subnivean space increases winter survival (Korslund and Steen,

2006). Thus, conditions in the subnivean space may markedly affect the dynamics of small rodents and their linked groups (Kausrud et al., 2008).

With decreasing duration of snow cover because of a warmer climate, species undergoing seasonal colour moults that are regulated by photoperiod risk being colour mismatched with their background. For example, it has recently been shown that this is indeed the case for the snowshoe hare (*Lepus americanus*) (Zimova et al., 2014).

Plant phenology is by and large determined by temperature, whereas appetite and reproduction in herbivores are determined by photoperiod, as outlined above. Thus, in Greenland, the onset of the plant growing season has advanced in response to warming – in some places by as much as 30 days (Høye et al., 2007). However, the timing of caribou calving has not advanced, which has resulted in increased mortality (Post and Forchhammer, 2008), probably caused by the mismatch between the earlier timing of the peak in plant quality and the appetite of the animal. Indeed, experimental work has shown that muskoxen appear to be unable to compensate for reduced food quality with increased food intake (Blix et al., 2012). However, the warming of the climate may not have negative consequences for all polar animals, because in Svalbard, for instance, the substantial ablation (see Glossary) associated with winter warming has resulted in reduced mortality, increased fecundity and increased abundance of reindeer (Tyler et al., 2008).

Conclusions

Polar animals show a number of behavioural, physical and physiological adaptations allowing them to maintain body core temperature in the cold. Small mammals with high mass-specific conductance and size constraints on the growth of thick fur curl up or huddle to reduce their exposed surface area, or seek shelter, and have, in addition to shivering, evolved mechanisms for non-shivering thermogenesis in BAT. BAT is also of paramount importance in newborn precocial mammals, but not in birds. Altricial young of both mammals and birds depend on parental care, and an extreme tolerance to cooling in the absence of their parents. Large mammals with low mass-specific conductance and thick fur or blubber insulation maintain core temperature by the cooling of peripheral tissues and appendages and by nasal heat exchange to save heat and water, before they resort to shivering.

Most polar animals prepare themselves for lack of food during winter by depositing large amounts of body fat during times of plenty in the autumn, and these stores are managed according to a sliding set-point for body fatness throughout winter. Some are able to reduce their energy expenditure at rest by the reduction of their basal metabolic rate and by reduced physical activity.

Both circadian and circannual rhythms in polar animals are regulated by photoperiod so that crucial processes, such as moulting, reproduction and body fattening, occur at the optimal time. Polar animals are primarily active during the light part of the day, but in the high Arctic, where the sun never sets in summer and darkness prevails during winter, the resident animals lose their daily rhythms and become intermittently active around the clock, allowing opportunistic feeding. This feature seems to be unique to high-latitude animals, whereas other traits are sometimes spectacular, but still only improvements of the responses seen at all latitudes.

Because global warming is particularly felt in the polar regions, understanding the basic needs and tolerances of polar animals to environmental change in terms both of physiological regulation at the individual level and genetic adaptation among populations is now of pressing importance.

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