# Animals at the extremes: Polar biology

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# Introduction

This course is the third in a series of three on *Animals at the extreme*. In order to get the most from it you should have previously studied**Animals at the extreme: the desert environment (S324_1)**and**Animals at the extreme: hibernation and torpor**

This OpenLearn course provides a sample of Level 3 study in Science.

# Learning Outcomes

After studying this course, you should be able to:

- define and use, or recognise definitions and applications of each of the bold terms
- outline the special features of the polar regions as a habitat and list some contrasts between the Arctic and the Antarctic
- describe some effects of daylength on feeding, fat deposition and reproduction in arctic animals
- explain why the environmental controls of appetite, activity level and fecundity are essential adaptations to living at high latitudes and describe some physiological mechanisms involved
- describe some adaptations of fuel metabolism and bone formation to dormancy in bears.

# 1 Polar biology

## 1.1 Preamble

This course is about animals' structural and physiological adaptations to living permanently in cold climates; hibernation, a special response to transient or seasonal cold, is described in the OpenLearn course *Animals at the extremes: hibernation and torpor* (S324_2). Living in a polar climate involves adaptations of many physiological systems: appetite, diet, energy storage and reproductive habits as well as thermo-regulation. In many cases, such changes involve 'ordinary' physiological mechanisms being pushed to extremes. The study of such physiological adaptations can help us to understand how humans and domestic animals could cope with similar conditions that arise under artificial or pathological conditions. For example, obesity is rare among wild animals, even when food is very plentiful, but in humans, the condition is common and often leads to numerous physiological complications, ranging from susceptibility to diabetes to mechanical damage to legs and feet. Most naturally obese animals occur in cold climates, and there is no evidence that they suffer from the complications of the condition that are observed in people and their domestic livestock. Perhaps we have something to learn about the natural regulation of appetite and the organization and metabolic control of fat from these cold-adapted species that have evolved ways of combining fatness with fitness.

On the evolutionary time-scale, modern polar environments, and hence living species of polar organisms, evolved relatively recently. The study of polar organisms provides the opportunity to study physiological adaptations of quite recent origin that evolved in organisms which were already complex and well-integrated. Such changes are comparable to artificial evolution in domestic animals, whether by manipulation of the genome (i.e. intensive artificial selection, gene transfer, etc.), or by drastically altering the diet and husbandry conditions. Polar organisms may help us to under-stand the physiological and psychological implications of the rapid, often drastic changes that we impose upon our own lives and those of our domestic animals.

Antarctica has been isolated from other continents since the Mesozoic supercontinent Gondwanaland broke up and the fragments that became India, Australia and New Zealand drifted away. The rich fossil record in Antarctica shows that a diverse tropical fauna, including early eutherian and metatherian mammals, once lived there. As the continent became colder, many species disappeared and adaptations to the climate evolved *in situ* in surviving lineages over many millions of years. Consequently, many of the organisms of Antarctica and the surrounding oceans are endemic.

In contrast, much of the Arctic is a large ocean, connected to the Pacific Ocean by the Bering Strait (that became a land bridge several times during the last million years) and through wider channels to the north Atlantic Ocean.

> When used as an adjective, 'arctic' generally refers to the regions around both Poles and does not have a capital letter. 'Arctic' and 'Antarctic' are the northern and southern arctic regions, respectively, and do have capital letters. To avoid confusion, the term 'polar' is used to mean both arctic and antarctic.

Prevailing winds and deep currents bring plenty of mineral nutrients to the Southern Ocean but the Arctic Ocean, particularly the areas north of Siberia, Alaska and Canada, is nutrient poor. Consequently, the Southern Ocean supports a much greater abundance of marine life than is found in most of the Arctic, except in a few areas such as the Barents Sea around northern Norway and northwest Russia.

Biological evolution in the Arctic has been much affected by the Pleistocene ice age, which produced several periods of glaciation over much of the Northern Hemisphere that began about a million years ago and continued until as recently as 10000 years ago. There were ice ages in the Palaeozoic and early Mesozoic, but until the Quaternary ice age began about 1 Ma ago, the climate had been mild, often warm, over the whole globe for the previous 250 Ma. The climate became colder and drier, promoting rapid evolution in many different lineages of animals and plants. Many species became extinct, but others, particularly descendants of cold-adapted organisms that lived on high mountains, adapted to the new conditions: numerous modifications of the skin and fur, endocrine mechanisms and behaviour and circulatory, respiratory, digestive and excretory systems evolved in many different species over a comparatively short period. Among them was an almost hairless primate, *Homo*, which adapted successfully to the cold climate in Europe and northern Asia after several million years of evolution in tropical Africa. Many such cold-adapted species ranged over much of the Northern Hemisphere until the climate became warmer during the interglacial period of the last 10 000 years, since when most have been confined to the Arctic.

## 1.2 The polar environment

At high latitudes, the Sun's rays always strike the Earth at a large angle from the vertical so they travel through a thicker layer of atmosphere and are attenuated by the time they reach the ground. Because the Earth's axis of rotation is inclined to its path around the Sun, there are large seasonal changes in daylength and the Sun is continuously below the horizon for a period in winter and continuously above the horizon for an equivalent period in summer. The annual changes in daylength and average temperature recorded just inside the Arctic Circle (at Tromsø, Norway) and far into the Circle (at Longyearbyen on the island of Spitsbergen, Svalbard Archipelago) are summarized in Figure 1. The range of annual temperature change is much greater at the higher latitude, and in mid-winter (January and February), the range about the mean is more than 12° C. In polar climates, the temperature can change abruptly and often unpredictably. In fact, both the localities featured on Figure 1 are on coasts, where the sea keeps the climate much more equable. Further inland, fluctuations in temperature are even greater. Polar organisms are thus adapted both to the extreme cold and to abrupt fluctuations in temperature.

The Arctic Circle (66° 30′N), and the equivalent latitude in the Southern Hemisphere, are defined as the latitude above which the Sun is continuously below the horizon for at least 1 day each year. Warm, moist air from the temperate zone rarely reaches high latitudes, so in most polar areas precipitation is low. Much of the water is locked away as ice, which has a low vapour pressure, and the air is very dry (often as dry as a tropical desert) and ground water is inaccessible to plants as well as to animals.

Terrestrial environments in the Arctic are, by geological standards, relatively new, most of the land having been completely covered with a thick layer of ice as recently as 10 000 years ago. Consequently, the soil is thin and fragile, and poor in organic nutrients. The optimum temperatures for plant growth do not coincide exactly with peak sunshine. At Longyearbyen, continuous daylight begins in late April, but the mean temperature does not rise above 0° C (and so the snow and ice do not melt) for another 2 months (Figure 1).

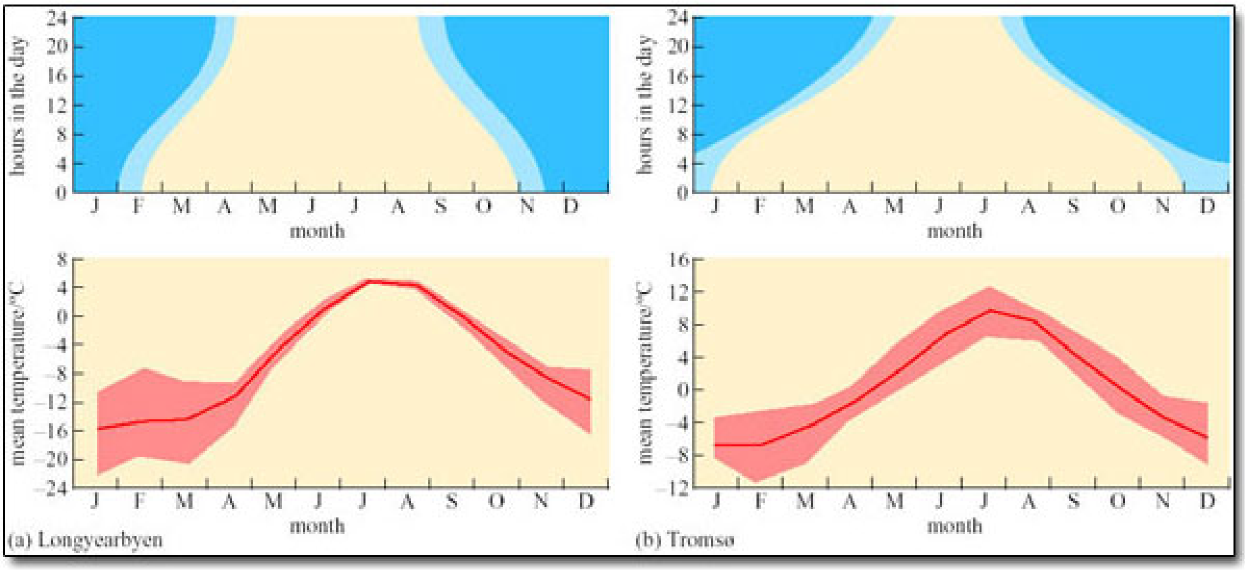


Figure 1 The number of hours of daylight (cream), twilight (light blue) and darkness (dark blue), and the mean temperature (red line) from January to December at (a) Longyearbyen, Svalbard (78° N), and (b) Tromsø, Norway (70° N). The pale red shading shows the range about the mean temperature

These circumstances, combined with the severe climate, mean that the growing season for plants is short but intensive, and total productivity on land is low, producing little food and still less shelter for animals. Consequently, relatively few species of terrestrial organisms live permanently at high latitudes. For example, although the land area of Svalbard is about 62 000 $km^2$, almost half that of England, there are only a few hundred species of insects and other invertebrates, two resident terrestrial mammals, the arctic fox (Figure 2a) and reindeer (Figure 2b), one bird (an endemic species of ptarmigan) and no reptiles, amphibians or completely freshwater fish. However, many other species spend part of the year on or near the land, often while breeding or moulting: seasonal visitors include more than 30 species of migratory birds (various kinds of geese, auks, puffins, skuas, terns, gulls, and eider ducks and snow buntings), and mammals that feed in the sea, such as polar bears, walruses and several species of seal. The simple ecosystem on land and the severe, erratic climate tend to produce ‘cycles’ of population abundance followed by mass mortality or migration (e.g. lemmings in Scandinavia and Russia). Interesting physiological and behavioural adaptations to these fluctuations in food supply have evolved in some of the larger animals. The vast continent of Antarctica has no indigenous terrestrial vertebrates, although many birds, including penguins, skuas, terns and gulls, and six species of seal spend time on or near land.

(a) (b)

Figure 2 (a) The arctic fox; (b) The subspecies of reindeer *Rangifer tarandus platyrhynchus*

Figure 2a: Dr Alison Ames; Figures 2b: Caroline Pond, Open University

Only two species of terrestrial mammal occur naturally throughout the year on Svalbard (although a few others have been introduced by humans during the past century). Figure 2a shows the arctic fox (*Alopex lagopus*), which also occurs throughout the Arctic, and in mountains at lower latitudes. The picture above, taken in late autumn, shows an adult in its long, dense winter coat. The summer coat is usually greyish brown, often with white markings. *Alopex* is bred in captivity for its fur, which can vary in colour from grey to bluish in winter, and chocolate brown to fawn in summer, hence the common names, silver fox or blue fox. Figure 2b shows a subspecies of reindeer (*Rangifer tarandus platyrhynchus*) that is endemic to Svalbard. This picture was taken in July, when the vegetation is at its highest, and these young males are growing antlers for the mating season in September

The situation in the sea is very different. Seawater freezes at −1.9° C, but because of the anomalous relationship between the density and temperature of water, ice floats, insulating the water underneath from the cold air above. Except in very shallow areas, the sea-ice does not extend to the sea-bed, even at the North Pole. Storms and currents sometimes break up the ice, creating many temporary, and some permanent, areas of open water even at high latitudes in mid-winter. Such turbulence also oxygenates the water and admits more light, making the environment much more hospitable to larger organisms.

The movements of ocean currents are complex (and may change erratically from year to year), often resulting in an upwelling of deep water rich in nutrients and promoting high primary productivity in the sea. In most arctic regions, the sea is both warmer and more productive than the land, so at high latitudes there are many more organisms in the sea than on land, at least during the brief summer, and, as in the case of the baleen and sperm whales, some are very large. Some groups of animals, such as bears, that are terrestrial in the temperate zone, have evolved adaptations that enable them to feed from the sea in the Arctic.

Sea-ice is less compact than freshwater ice, and contains many tiny channels containing liquid water as well as cracks caused by weather and currents. Hence sea-ice appears opaque rather than transparent like freshwater ice. The pores harbour a variety of single-celled algae, bacteria and other microbes that form the basis of surprisingly productive food chains. Most of those living on or near the surface are photosynthetic, and during the summer, such microbes are dense enough to confer a brown colour on the underside of the sea-ice. These organisms, and similar ones living on snow and in cold, dry terrestrial habitats, are collectively known as **psychrophiles** (ψυχροσ, *psychros*=cold, Φιλοσ, *philos*=friend). The continent of Antarctica is generally much colder at comparable seasons and latitudes than most of the Arctic, with the possible exception of large landmasses such as Siberia, Alaska and some of the bigger islands off the north coast of Canada. With its harsher climate, and longer period of biological isolation, Antarctica has a wider variety of endemic, impressively adapted psychrophiles than most of the Arctic.

# 2 Environmental regulation of physiological processes

## 2.1 Nutrient budgeting

All plants and animals respond to environmental changes such as the light–dark cycle and temperature, but the impact of the environment on essential physiological processes such as eating, fattening and breeding is more evident and often more finely controlled in polar species than in those that are native to warmer and more equable habitats. Large effects are nearly always easier to quantify and to investigate experimentally, so arctic species offer an excellent opportunity to study the subtle but often important action of environmental changes on physiological processes.

A good place to begin such an analysis is with nutrient budgeting. Energy is expended in the search for food, and in ingesting and digesting it. If food is so scarce that searching is inefficient, or its nutrient content so low that little nourishment is obtained from it, animals may be able to save energy by suppressing appetite and fasting. In polar environments, food is widely scattered both in space and in time. Consequently, the physiological mechanisms that regulate appetite and energy storage are sophisticated and effective in arctic species. Herbivorous animals such as reindeer are directly dependent upon plant productivity and synchronize their foraging and other energetically expensive activities, such as mating and breeding, with it. Daylength (photoperiod) is a more reliable indicator of season than temperature (see Figure 1) and is often an important regulator of physiological mechanisms.

To investigate seasonal changes in the behaviour and metabolism of species native to the high Arctic, a few adults of the subspecies of reindeer that is endemic to Svalbard (*Rangifer tarandus platyrhynchus*, see Figure 2b) were transported to northern Norway and kept in small outdoor pens there, alongside similar individuals of the native subspecies, *Rangifer tarandus tarandus* (Larsen et al., 1985). All the animals had continuous, unrestricted access to forage but, as shown on Figure 3, the Svalbard reindeer ate three times as much food in August as in March.

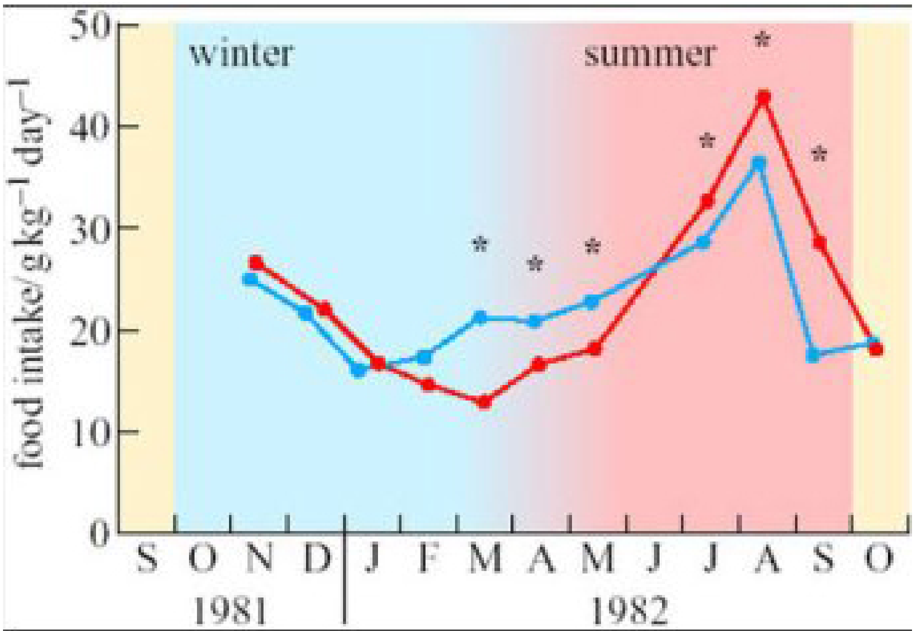


Figure 3 Seasonal changes in the voluntary food intake (in grams per kg body mass per day) of Norwegian reindeer (blue) and Svalbard reindeer (red) with unrestricted access to food. Asterisks mark significant differences ($P < 0.05$) between subspecies

SAQ 1

Are these seasonal changes in the appetite of Svalbard reindeer simply a direct response to the environment?

Answer

No. There were seasonal changes in the food eaten by local Norwegian reindeer as well, but they were less pronounced than those of the animals native to high latitudes. In addition, the largest differences between the two subspecies were observed in mid-March and mid-September, around the equinoxes when day and night are equal in length over the whole globe.

SAQ 2

Do seasonal differences in energy expenditure explain these data?

Answer

No. Being confined in small pens, the reindeer took little exercise all the time. Energy expended on thermoregulation should be greater in cold weather, so if thermogenesis was important, one would expect them to eat more, not less, in the winter.

Reindeer (Figure 2b) grow thick coats of long, hollow hair that insulates the warm skin so effectively that snow accumulates on their backs without melting. Energy expenditure on shivering or other forms of thermogenesis seems to be minimal even in the coldest weather. Foraging is slower and less efficient in winter, and the lower total daily intake is supplemented by utilization of the fat reserves built up during the brief summer, when they eat almost continuously. However, as these experiments show, the seasonal changes in food intake arise primarily from the endogenous control of appetite, and are not imposed upon the animals by food availability. The fine control of appetite is slightly different in subspecies adapted to different climates. The investigators also found small but significant differences at certain times of year between Norwegian and Svalbard reindeer in the rates of lipogenesis measured in adipocytes *in vitro*, and in the responses of adipose tissue to hormones such as adrenalin.

Metabolic rate, food intake and other aspects of energy balance also change seasonally in birds and mammals that are native to high latitudes. The red, or common, fox (*Vulpes vulpes*) occurs throughout Europe and northern Asia except in high mountains and arctic regions, where it is replaced by the smaller arctic fox, shown in Figure 2a. As shown on Figure 4a, at above 10° C, the fox's basal metabolic rate (BMR) is about the same in summer and winter, but as the temperature falls, the rise in BMR is delayed and is slower in winter-adapted animals than in those caught in summer.

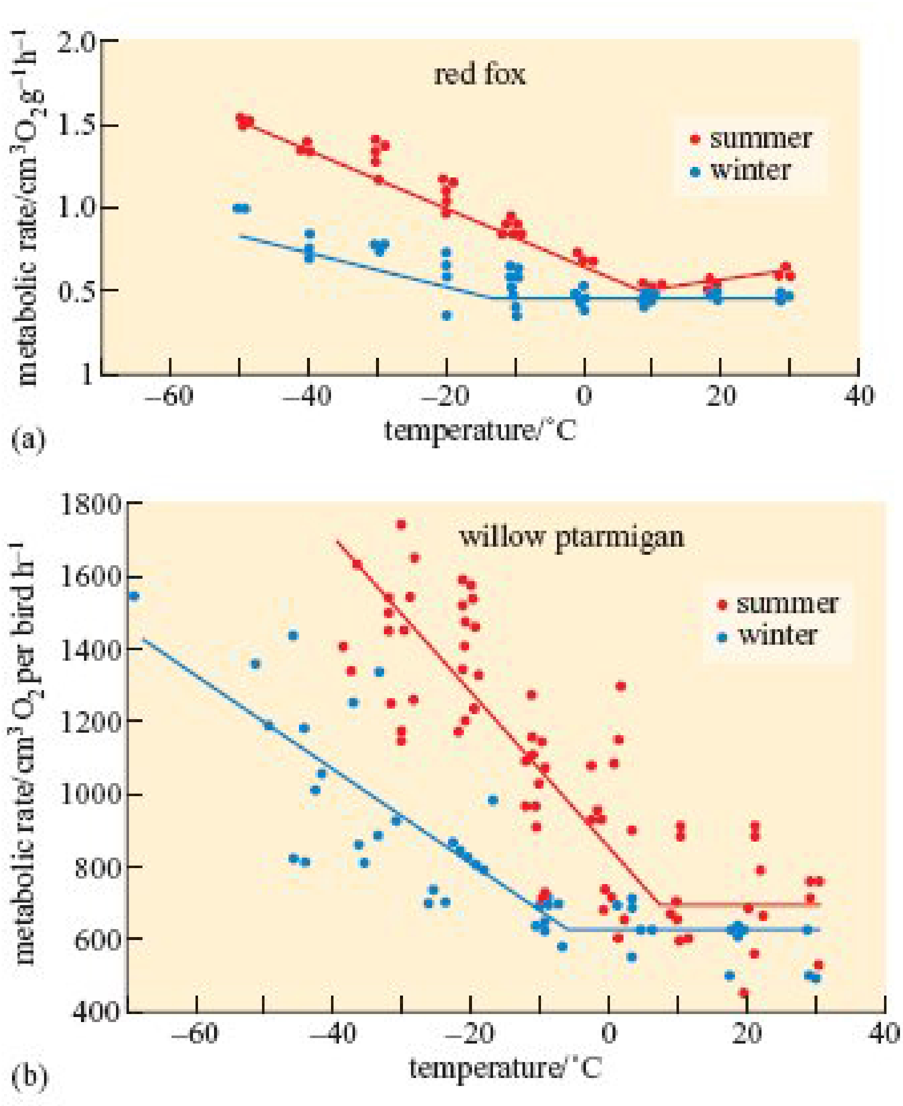


Figure 4 The resting metabolic rates at different temperatures of (a) red fox and (b) willow ptarmigan acclimatized in captivity to summer and winter conditions. The adult body mass of foxes is 3–7 kg

Such phenomena have been intensively investigated in ptarmigan (Figure 5) which are non-migratory, mainly ground-dwelling grouse-like birds that eat twigs, shoots and other plant material. There are two species in Scandinavia and Russia: the willow ptarmigan (*Lagopus lagopus lagopus;*Figure 5) and the rock ptarmigan (*L. mutus mutus). ('Lagopus'* means 'foot of a hare' and refers to the feather-covered or fur-covered feet of the ptarmigan and arctic fox, see Figures 2a and 17.)

Figure 5 A willow ptarmigan (*Lagopus lagopus lagopus*) in winter plumage, with the arctic willow bushes on which they feed. This photograph was taken near Churchill, Manitoba, on the western shore of Hudson Bay, Canada in late October

Dr Alison Ames

A subspecies of rock ptarmigan occurs only on Svalbard; it is larger than the mainland forms, and has almost pure white plumage during the 8 months of winter. As shown on Figure 4b, the metabolic rate of willow ptarmigan measured at a wide range of temperatures is lower in winter than in summer. The seasonal differences are even greater in Svalbard ptarmigan (L. *mutus hyperboreus*). Svalbard ptarmigan also eat much more in the late summer than in winter and accumulate fat in the autumn. The experiments summarized in Figure 6 reveal some of the physiological mechanisms that control these changes in appetite and energy storage (Lindgård and Stokkan, 1989).

When exposure to continuous light was started in July (Figure 6a), the birds' usual autumnal fattening proceeded as normal, but their body mass remained high and food intake fairly low, right through to the following September.

Throughout this period, their plumage remained white and they failed to breed. It was as though the continuous light held them indefinitely in their autumnal condition. However, when exposure to continuous light was started in November (Figure 6b), the birds underwent a complete cycle of changes in body mass and food intake (and began to develop speckled summer plumage) before settling into continuous high body mass and low appetite.

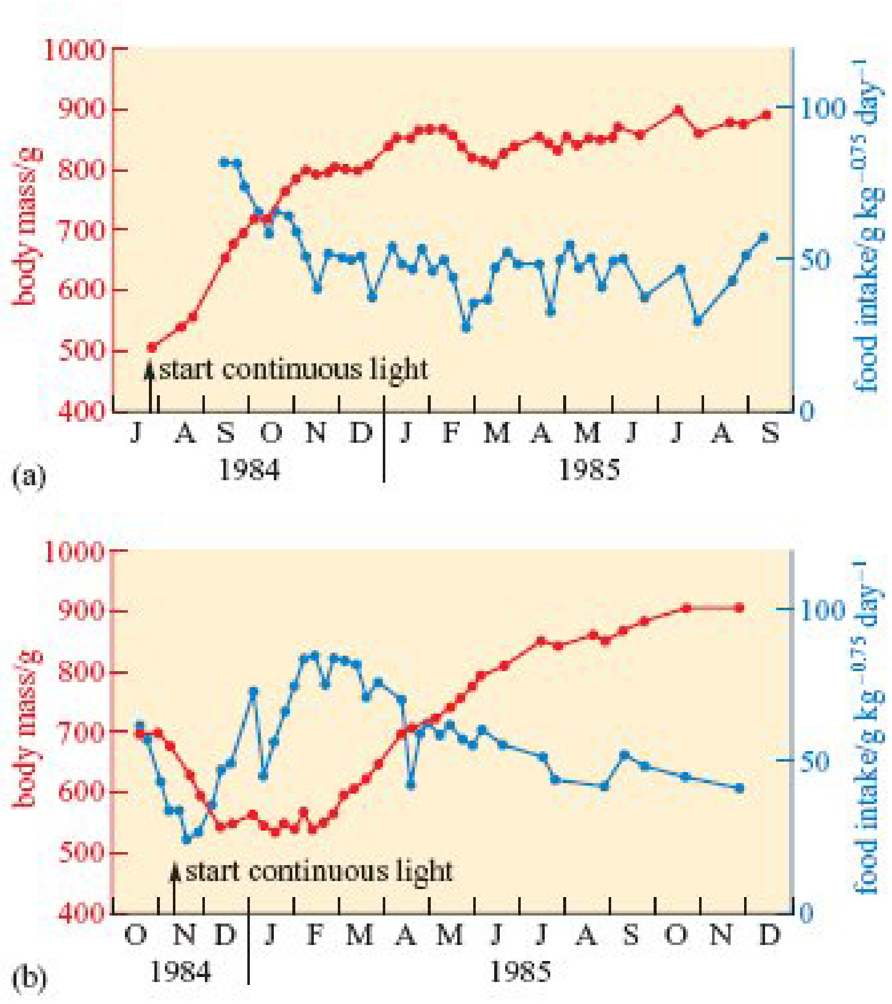


Figure 6 Changes in food intake (blue lines) and body mass (red lines) in Svalbard ptarmigan during 15 consecutive months kept in captivity with unlimited access to food at Tromsø. (a) Birds kept outside and then indoors in continuous light from July onwards, (b) Birds kept outside and then indoors in continuous light from November onwards

SAQ 3

What do these experiments show about how seasonal changes in appetite and body mass are controlled?

Answer

They are not simply a response to environmental conditions but are at least partly controlled endogenously.

Exactly how such control mechanisms evolved and what happens when animals (or people) are abruptly transported into environments in which their endogenous controls of appetite and energy expenditure are inappropriate are not known.

Although several ruminant mammal species live in mountains and arctic regions (e.g. mountain goats and reindeer, respectively), none is known to hibernate in the strict sense of the term. There are no living species of the family Bovidae smaller than sheep or goats, but some deer (family Cervidae) are less than a tenth of that size as adults. Some tropical deer, notably species of mouse deer *Tragulus*, weigh only 1–2 kg, well within the range of size of mammals that can become torpid, but none is known to do so.

One reason might be that substantial changes in body temperature would kill the microbes in the rumen that are essential to digestion. Another possibility is that in ruminants, both storage and membrane lipids contain mostly saturated lipids, which have a higher melting point than unsaturated lipids. Laboratory experiments in which animals were fed diets rich in saturated or unsaturated lipids just before hibernation showed that, at least in small rodents, a larger proportion of unsaturated lipids in cell membranes and adipose tissue is essential to successful hibernation . Finally, pregnancy, which lasts a relatively long time in ruminants and usually takes place during the winter, could not be sustained at very low body temperatures.

## 2.2 Migration for breeding

Birds do not hibernate, but like reindeer, many species undergo daily or seasonal changes in energy expenditure and appetite, and many of the endocrine changes that are an integral part of true hibernation in other groups. The fact that the preliminary stages of hibernation are widespread among vertebrates may help to explain why true hibernation has evolved several times in distantly related taxa. Instead of hibernating, some species of birds migrate to and from breeding areas, where they are able to exploit transient gluts of vegetation or, more often, of the insects and other arthropods that feed on them. Long-distance migratory birds belong a wide variety of taxa, including cranes (order Gruiformes), swifts (order Apodiformes), some swans, ducks and geese (order Anseriformes), cuckoos (order Cuculiformes) and many different kinds of passeriform birds including swallows and martins (family Hirundinidae).

Some birds travel to the Arctic to breed during the polar summer, which can be both cool and short at very high latitudes (e.g. Svalbard), or in regions such as Siberia that have particularly severe climates. It's worth mentioning in passing that until these remote regions were explored in the 18th and 19th centuries, the breeding sites of many migratory birds were a complete mystery, giving rise to wild speculations about where, if at all, the birds bred. For example, barnacle geese (*Branta leucopsis*) derive their name from the medieval belief that they arose spontaneously from barnacles. In fact, they breed in Greenland, Svalbard, remote parts of Sweden and northern Russia, with almost all the Svalbard population spending the winter around the Solway Firth and Dumfries and Galloway, Scotland. Red knots (*Calidris canutus*, order Charadriiformes) are 'waders', eating worms, shellfish and other invertebrates collected from beaches, mudflats and estuaries. These small birds (adult body mass about 0.1 kg) form large, dense flocks near sandy or muddy coasts of northern Britain and northwest Europe during the winter (Figure 7). Like many birds, the juveniles eat insects and other small arthropods. Some populations breed between June and August on the Taimyr Peninsula, the most northerly region of Siberia that extends into the Arctic Ocean. The area became free from permanent ice following the end of the last ice age only a few thousand years ago, and is flat and marshy, with several large slow-flowing rivers that support huge populations of mosquitoes and other insects in summer.

Figure 7 A red knot (*Calidris canutus*) feeding on the north coast of Norfolk near The Wash in early September. This adult's rust-red breeding plumage is fading into the inconspicuous white and grey winter plumage. It has probably recently returned from breeding in the Arctic

Mark Eaton

### SAQ 4

What would be (a) the advantages and (b) the disadvantages of breeding in such places?

#### Answer

(a) Advantages: fewer predators (though arctic foxes, snowy owls and large gulls such as skuas are present); foods suitable for the chicks and adults are available in large quantities in adjacent habitats; continuous daylight (Figure 1) permits continuous foraging. (b) Disadvantages: the weather is often cold and stormy, and the terrain offers little shelter, so keeping the eggs and chicks warm may pose problems. The breeding season is very short, necessitating rapid growth of the chicks. The journey between Siberia and northwest Europe is tens of thousands of kilometres.

Dutch ornithologists used doubly-labelled water and other techniques to study the growth and metabolism of chicks there, and compared their data to similar observations on other species of the order Charadriiformes with similar habits (sandpipers, dunlins, turnstones, godwits, plovers and oystercatchers) that breed in the temperate climates of northwest Europe (Schekkerman et al., 2003). They found that chicks of the arctic-breeding species both grew faster and generated more body heat, mainly by shivering, than similar birds breeding in temperate climates. The increased thermogenesis was necessary not only because of the severe climate, but also because in Siberia, the parents actually spent less time brooding even very young hatchlings. Red knot chicks are precocious and can forage for themselves at a few days old. They apparently also manage with very little sleep (in sharp contrast to most neonatal birds and mammals, which require many hours of sleep), enabling them and their parents to forage for up to 20 h per day. The total energy expenditure from hatching to fledging was found to be up to 89% higher in the arctic-breeding knots, but the chicks were dependent on the parents for only 17–20 days, a shorter period than related species of similar size.

This study demonstrates a range of far-reaching adaptations of thermoregulation, growth rate and sleep requirements in birds that breed in polar regions. The opportunity to exploit the temporary abundance of food apparently outweighs any disadvantages associated with these adaptations of growth rate and thermogenesis and the energetic costs of migration.

The journey itself requires further metabolic specialization. The birds break their journey at several places where food is abundant and easily obtained. However, since time is short, some stopovers last as little as 1–4 days, during which time they must take on enough fuel for the next stage of the journey. The closely related sandpiper (*Calidris mauri*) that also breeds in the Arctic can fatten at 0.4 g $day^{-1}$ (4.5 times the normal rate) during brief stopovers. This remarkably high rate of deposition of fat stores is possible due to a temporary increase in the activity of lipogenic enzymes such as fatty acid synthase.

## 2.3 Environmental regulation of breeding

As pointed out in Section 1.1, primary plant productivity occurs for only a few months in the summer, so the reproductive physiology of most arctic animals, particularly herbivorous species, is tightly synchronized with the seasons. On Svalbard (Figure 2b), more than 90% of the reindeer fawns are born in the first week of June. The mothers of those born too soon or too late are often unable to find enough food to support lactation and the fawn fails to thrive. As shown on Figure 1, the onset of continuous daylight and that of the conditions that support plant growth are several months out of phase. This situation poses little problem for reindeer, because the duration of pregnancy is almost constant and they mate only during a brief rutting period in September, when the daylength is changing rapidly. But this environmental cue alone would not be an accurate control on the timing of breeding of resident herbivorous birds such as ptarmigan that breed in mid-summer.

The physiological mechanisms that control the timing of several aspects of mating and breeding in the Svalbard ptarmigan (*Lagopus mutus hyperboreus*) have been investigated in detail (Stokkan et al., 1986). Their plumage is almost pure white in winter but speckled brown feathers appear in summer and the adult males have a red fleshy ‘comb’ over each eye. Figure 8 shows the seasonal changes in these secondary sexual characters, the maturation of the gonads, and the concentration of luteinizing hormone (LH) in blood plasma in ptarmigan shot on Svalbard. LH levels (Figure 8a) are low from August until February, when the Sun reappears (see Figure 1). The blood plasma LH levels and body mass (see Figure 6) start to increase slowly, and in March first primary, then secondary, spermatocytes appear in the testes (Figure 8b) and the combs begin to grow (Figure 8c). However, there are no mature spermatozoa until the end of May, so the gonads mature much more slowly than in most other seasonally breeding birds. Pigmented feathers also do not appear until June, just before the snow melts (Figure 8c).