FIG 69. Golden Plover *Pluvialis apricaria*, whose body composition varies greatly between the autumn and spring migrations, with much more protein accumulated prior to spring migration, in preparation for breeding. (Edmund Fellowes)

example, the 40–50 g mass gain by 200 g European Golden Plovers during stopovers consists almost entirely of fat in autumn, but mainly of protein in spring. These birds have different needs at the two seasons. They face energy deficits in autumn and winter when they eat mainly protein-rich earthworms, but they risk protein deficits in spring, for after arrival in their arctic breeding areas they eat mainly berries left from the previous year but must soon produce eggs (Piersma & Jukema, 2002).

At least 5–10 per cent of the total energy released during a migratory flight must come from protein, which is used in the biochemical processes that break down fat (Jenni & Jenni-Eiermann, 1998). So the amount of protein metabolised during a flight depends partly on the amount of fat used. The

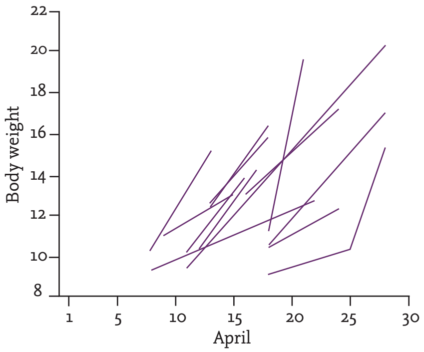

FIG 70. Body mass changes, reflecting pre-migratory fuel deposition, in Sedge Warblers *Acrocephalus schoenobaenus* caught repeatedly in spring 1971 near Nairobi in Kenya. The maximum rate recorded was for a bird which went from 11.2 g to 19.6 g in three days, a 75 per cent increase. Another bird more than doubled its weight in 17 days. For most individuals this site may have provided their last feed before crossing the Sahara desert. (From Pearson *et al.*, 1979.)

TABLE B. Energy and water yield of the three main fuel types in birds. *Note*: One kilojoule (kJ) is equivalent to 0.24 kilocalories, and a kilocalorie is popularly called a 'calorie' in human dieting. (Modified from Jenni & Jenni-Eiermann, 1998)

	Lipids in adipose tissue	Protein in skeletal muscle or digestive organs	Glycogen
Energy density (kJ g^{-1}) in dry mass	39.6	17.8	17.5
Energy density (kJ g^{-1}) in wet mass	37.6	5.3	3.5–4.4
Water content (%)	5	70	75–80
Metabolic water production (g water per g dry matter)	1.05	0.39	0.56
Total water production (g water per g wet tissue)	1.10	0.82	0.89–0.91
Water produced (g water per kJ expended from wet mass)	0.03	0.16	0.21–0.25

protein is derived partly from the flight muscles, but also from other muscles, and from other organs such as the gut (Piersma & Gill, 1998). The metabolism of protein is less efficient than that of fat and carbohydrate, and also produces toxic by-products. Moreover, in contrast to fat, which is stored 'dry', the storage of each gram of protein requires around 4 g of extra water. This can be a substantial weight burden, but it may help to counter dehydration on long non-stop flights (Table B).

The third source of energy, carbohydrate, is stored as glycogen in the liver and muscle tissue, but when some birds prepare for migration, they change from using mainly glycogen for energy to using mainly fat (Dolnik & Blyumental, 1967; Jenni-Eierman & Jenni, 1996). At migration times, therefore, carbohydrate is of relatively minor importance as an energy source. The highest glycogen values reported from birds amount to no more than about 3 per cent of liver mass and about 0.5 per cent of total body mass (Marsh, 1983; Blem, 1990). Despite being stored 'wet', glycogen in such small amounts is also of little value as a water source.

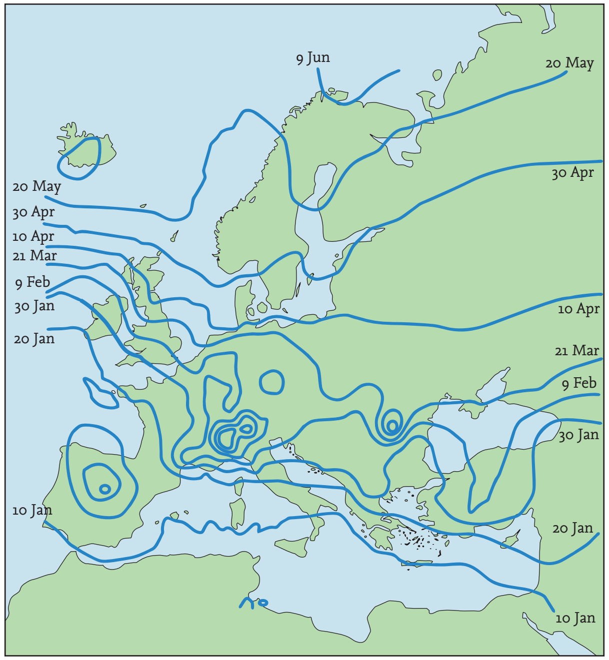

FIG 113. The advance of spring, as shown by the dates that the rising 10°C isotherm reached different parts of Europe, based on average values for 1971–2000. (Adapted from T. H. Sparks, unpublished.)

Variations in spring migration dates

The dates at which most bird species move northwards through Europe in spring depend partly on the food supplies that become available at successive latitudes. Migrating birds need food not only for daily maintenance, but also to fuel successive stages of their journeys (Chapter 6). There would normally be no advantage for migrating birds to arrive before their developing food sources, as they would then only lose body condition, and might even have to turn back (as sometimes happens; see Chapter 4). However, migration dates are largely an evolved response to past conditions (Chapter 15), so they cannot be expected to precisely match food supplies every year. In cold years, birds sometimes arrive 'too early', and many starve to death, as described in Chapter 23.

As some types of food become available earlier in spring than others, different species arrive at particular localities in fairly consistent sequence from year to year, and at roughly similar dates. Species that depend on spring thaw to release their food supplies (such as some waterfowl and waders) arrive earlier than those that rely on aerial insects (such as hirundines), and earlier still than those that depend on larval insects from later-developing leaves (such as some warblers).

FIG 114. Long-tailed Ducks *Clangula hyemalis* (left) and Scaups *Aythya marila* (below), which winter on the seas around the British Isles, arrive in their arctic nesting areas in early June, as soon as open water becomes available there. (Edmund Fellowes)

LATITUDINAL TREND IN ARRIVAL DATES

In the first half of the 20th century, much attention was given, with the help of observer networks, to recording the northward advance of various bird species in spring (Fig. 115). In general, earlier migrants spread northwards more slowly than later ones. Five trans-Saharan migrants, namely the Barn Swallow, Willow Warbler, Common Redstart, Wood Warbler and Red-backed Shrike, arrived in southern Europe on the progressively later dates of 13 February, 5 March, 15 March, 1 April and 1 April respectively. They spread north through western Europe at average speeds of about 40, 46, 66, 70 and 88 km per day, and took around 109, 88, 61, 45 and 45 days to get from the southern to the northern parts of their breeding ranges (Southern, 1938–41). Their northward progression generally kept step with

CHAPTER 18

Geographical Patterns

Of all the types of movements undertaken by birds, regular seasonal migration is the most impressive, partly because of the enormous numbers of birds involved, and partly because of the huge geographical scale it encompasses. Associated with seasonal fluctuations in climate and food supplies, migration leads twice each year to massive changes in the distribution of birds over the earth's surface. High-latitude regions receive birds mainly in the breeding season, while lower-latitude regions support wintering birds from higher latitudes, as well as year-round residents. Some species occupy habitats over winter that they could not use for breeding, and then establish themselves in breeding areas that would not support them in winter. This applies, for example, to all Arctic-nesting shorebirds which occur in winter on coastal mudflats where, due to tidal flooding, nesting would be impossible; they then migrate north to breed on the Arctic tundra which is frozen and snow-covered for the rest of the year. Migration thus increases the numbers of species found in particular regions, even though some are present for only part of the year.

LATITUDINAL TRENDS

In general, the proportions of bird species that leave their breeding areas for the winter increase from low to high latitudes, as the contrast between summer and winter conditions widens (Newton & Dale, 1996a, 1996b). Progressing northward up the western seaboard of North Africa and Europe, the proportion of breeding bird species which move out totally to winter further south increases from 29 per cent of species at 30°N (North Africa) to 83 per cent of species at 80°N (Svalbard), a mean increase of 1.3 per cent of breeding species for every degree of latitude (Fig. 193).

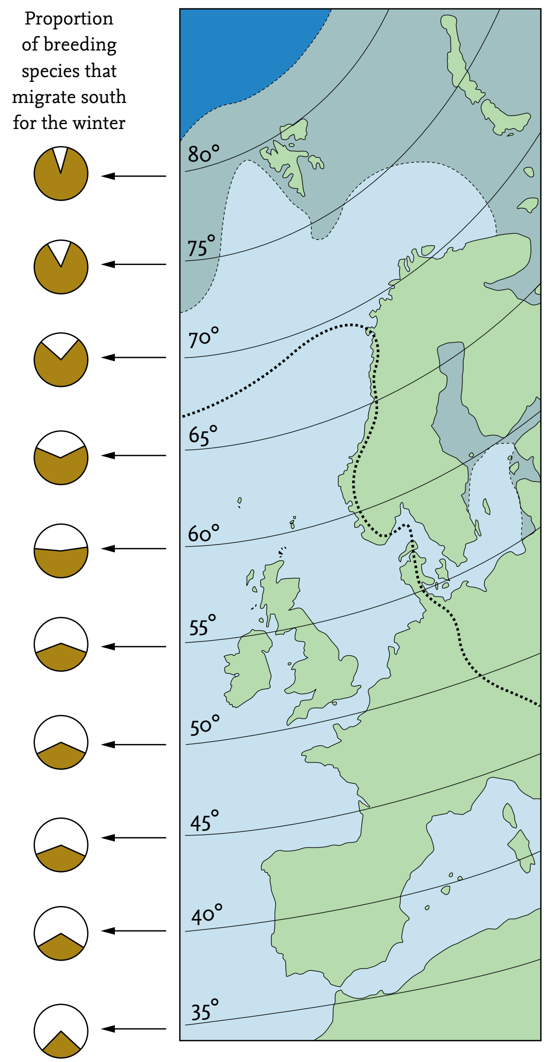

FIG 193. Map of western Europe showing the proportions of breeding bird species at different latitudes that migrate south for the winter. Legend: dark blue – permanent ice; grey blue – winter ice; dotted line – 0°C mean January isotherm. (From Newton & Dale, 1996a.)

This geographical trend holds, it has been suggested, because the winters are so harsh at high latitudes that very few species can remain there year-round. In consequence, the flush of food in summer is greater than the small number of resident birds can exploit, leaving a surplus available for summer visitors. These summer migrants increase in proportion with latitude, as the severity of winters increases and the numbers of year-round residents decline. At lower latitudes, a high proportion of breeding species can remain year-round, leaving fewer openings for summer visitors. Whatever the explanation, a similar relationship between migration and latitude holds in the largely different avifauna of eastern North America (Newton & Dale, 1996b), and presumably throughout the northern hemisphere. It also holds in the southern hemisphere, although no comprehensive study has yet been made (Newton, 2008).

Let us examine winter conditions in more detail. In Europe, over much of the 20th century, mean January temperatures exceeded 10°C only in southern Spain; they lay within the range 0–5°C in much of western Europe, but fell below freezing and as low as -15°C in most of Fennoscandia, plunging to -20°C in Novaya Zemlya in the far north. Minimum winter daylengths were around 11 hours at 35°N in southern Europe but decreased to zero at the Arctic Circle. The season of plant growth lasted six to nine months at 35–50°N (mainly Spain and France), but shrank to less than three months in Svalbard, a mean decline in growing season of about one month for every 11° of latitude. In continental western Europe, most fresh waters north of 56°N (latitude of Copenhagen) froze in winter, remaining open for most of the time in Britain and Ireland. Much of the Baltic and Barents Seas also iced over during the course of the winter, closing these areas for seabirds. Throughout much of this region, however, temperatures are now rising as part of human-induced 'global warming'. Bird migration patterns are changing accordingly (Chapter 16), but they still relate to geographical gradients in prevailing conditions.

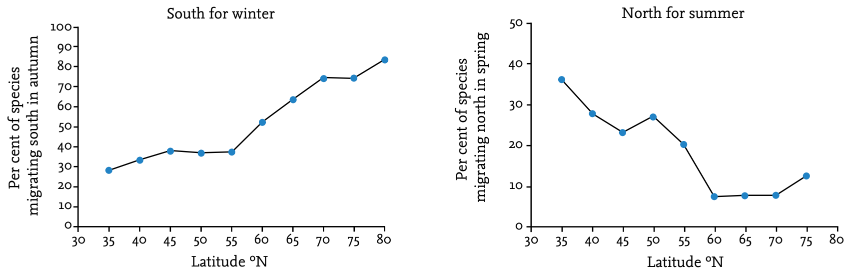

FIG 194. Proportions of breeding bird species (y-axis) at different latitudes (x-axis) in western Europe that (a) migrate south for the winter or (b) north for the summer. For southward migration, on regression analysis for western Europe: $y = 41.49–1.03 + 0.02x^2$, $r^2 = 0.97$. For northward migration, on regression analysis for western Europe: $y = 55.65–0.66x$, $r^2 = 0.81$. For the first of these relationships, a quadratic equation gave a significantly better fit than a linear one. Because 23 species leave Europe altogether in winter, spending their non-breeding period in Africa, the figures for the southward and northward migrations do not exactly match. (From Newton & Dale, 1996a.)

FIG 195. Gyrfalcon *Falco rusticolus* (immature), one of the few bird species in which most individuals remain in the arctic year-round. It is a rare winter visitor to the British Isles: white-phase birds, like the one shown, are likely to derive from Greenland or eastern North America, and dark-phase ones from Iceland or northern Europe. (Cal Sandfort)

The few species that remain to winter in the far north include the Common Raven, Rock Ptarmigan, Gyrfalcon and Snowy Owl among land birds, and the Northern Fulmar and Glaucous Gull among seabirds. The most northerly seabirds depend in winter on the open water provided by polynyas, where surface currents are too strong to permit freezing, and some of the gulls also scavenge the remains of seals killed by polar bears. Some individuals of these species probably move south to some extent in the weeks of complete darkness.

The converse of these latitudinal patterns is shown in Figure 194 as the proportions of the species wintering at different latitudes that move north for the summer. As expected, this proportion is greatest in the south: in western Europe, affecting 36 per cent of species wintering at 35°N (northernmost Africa), declining northward to 8 per cent of species wintering at 70°N (northernmost Norway, mostly seabirds), with none at 80°N (Svalbard). The precise relationship varies somewhat between birds of different habitats, with aquatic species being especially responsive to freezing. In addition, 23 per cent of all species breeding in western Europe vacate the continent completely in autumn for the tropics, returning in spring (Newton & Dale, 1996a).

The proportions of all bird species that are migratory are correlated not only with latitude, but also with various climatic factors that vary with latitude, such as the temperatures of the hottest or coldest months, or the temperature difference between the hottest and coldest months (Newton & Dale, 1996a). These various measures are of course interrelated, but what matters is the extent of climatic difference between summer and winter. It is this difference that, for many birds, governs the difference in food supply between summer and winter at particular latitudes, and hence the difference in the ability of the local environment to support birds at the two seasons. Over a geographical