Birds can only occur where they can find sufficient and suitable food. Bird species are not free to choose their diet, as a herbivore requires a different gastro-intestinal tract (as well as the necessary digestive enzymes) to a carnivorous species. The mode of nutrition is thus determined both genetically and phylogenetically. If the ancestor of a species were piscivores it is rather unlikely that a direct descendant would become a granivore. These are, of course, trivial facts but they are significant in answering the question as to how the phenomenon of bird migration originated.

Birds were especially successful in evolution because they were able to settle in almost all habitats on the planet, which differ particularly in the available potential dietary resources. One of the preconditions was not only anatomic adaptation such as flight, walking, or diving capabilities, but a specialisation to the available food source. If therefore a region or habitat was rich in fish, species from the guild of piscivores could settle and diversify there. For herbivores on the other hand, such a region or habitat would offer little or no possibilities for development.

**The influence of the Ice Ages on flora and fauna**

The geographical distribution of food resources is not immutable but depends on the climate that over the past million years (in the Miocene and Pleistocene periods) has experienced regular changes of warm and cold periods (a cycle of some 100,000 years). The vegetation in the northern hemisphere today, which we accept as natural, is young in terms of the Earth’s history.

Some 18,000 years ago as the last ice age in Europe reached its furthest geographic extent, a thick layer of ice covered large areas of the continent. The temperatures in the ice-free regions were similar to those in the Arctic today. In wide areas of Europe therefore, there was no deciduous woodland or grassland but rather a steppe-tundra inhabited by reindeer, mammoths, and other arctic animal species.
species. During the ice age, Africa experienced widespread drought with an extensive expansion of the Sahara and a great reduction in the size of the rainforests.

The last ice age ended some 12,000 years ago when the glaciers and ice sheet melted. The released melt water caused a rise in the sea level of some 120–130 m. At that stage, the North Sea as we know it today was formed and the land bridge to Britain was submerged. Deciduous mixed woodland took the place of the tundra-steppe vegetation in Central Europe, which withdrew to Northern Europe. Some 10,000 years ago there was increased rainfall in the Sahara region and for several thousand years (until about some 5,000 years ago towards the end of the height of the Holocene) the Sahara was a green and fertile savannah rich in flora and fauna. Only after this period did the Sahara revert again into the desert and ecological barrier that we know today. Food availability and the distribution and migratory behaviour of bird species are closely related.

» Herbivores

Although plant biomass is available in large quantities only relatively few groups of birds specialise in this food resource. An animal or bird would have to consume large quantities of low-energy leaves or grasses to become sated and also be capable of metabolising the normally indigestible cell wall components and poisonous secondary metabolites. Among mammals, ruminants and other hoofed animals have evolved into particularly specialised herbivores. The price of this however, was an increase in body size and, in ruminants, the development of a voluminous ruminant stomach with specially adapted microorganisms capable of breaking down cellulose. For birds, whose bodily frame must remain light in order to fly, the development of a ruminant stomach was clearly not a sustainable option. The Palaeognathae, or ratites such as the Ostrich, Emu, and Rhea, which are all herbivores and today have a generous body weight, mark the start of the phylogeny of modern birds. The ratites became flightless at an early stage. Many species of Galloanserae (i.e. swans, geese, ducks, and galliforms – that phylogenetically follow the Palaeognathae) have widely retained their herbivorous diet; only a few species have become piscivores or insectivores. Green plant material is however, also con-
sumed by representatives of the bustard, crane, and rail (Coot and Moorhen) families. Seeds and fruit, in which some bird families such as grouse, doves, sparrows, many passerines, finches, and buntings have specialised, are significantly richer in energy.

Bird species that have specialised in leaves, needles, and grasses, find food almost the whole year round in Central Europe. It is therefore not surprising that almost all Phasianidae (grouse, partridges, and pheasants) are resident birds in Central Europe.

Arctic-breeding geese and swans find no nourishment in their breeding areas in winter; they migrate southwards and winter on the coasts of the North Sea or the large lakes in Central Asia, where sufficient food is also available in winter. It should not be forgotten however that the arctic breeding grounds became accessible only from about 10,000 years ago, after the end of the last ice age. During the last ice age, insofar as it was not covered in ice, an extensive steppe-tundra existed in Central Europe. The Nordic geese that today settle the Arctic probably bred in this Central European tundra. As the climate in Central Europe changed in the post-glacial period, and with it the vegetation, the geese and swans shifted their breeding grounds more and more northwards. There they found abundant food resources without a great deal of competition. In order to escape the arctic winter, migration evolved from the Arctic into climatically more favourable areas to the south. In Central Europe, plants do not produce seeds all the year round but rather at the end of the vegetation period from late summer until early spring. This food resource is therefore generally not available to granivores throughout the year. Granivores however, also consume animal food (arthropods) that is abundantly available during the summer half-year. Many Central European granivore and insectivore species (woodpeckers, tits, nuthatches, sparrows, finches, and buntings) find food the whole year round and are therefore frequently resident birds. The local populations are however, supplemented by new arrivals from Northern and Eastern Europe when these areas experience periods of heavy frost or heavy snow cover. In these conditions seeds are hard to find. Granivores are seldom long-distance migrants to sub-Saharan Africa.

The Arctic Tern is an exceptionally long-distance migrant, breeding in the Arctic and wintering in the Antarctic, and covering annually up to 40,000 km on its migration flights.
Matters are similar for frugivores, as fruit is available from summer until early winter. Fruit is available throughout the year only in the tropics and it is there that the greatest diversity and variety of frugivores species can be found. Of our birds, thrushes, waxwings, and some warbler species are characteristic frugivores that eat fruit temporarily but are otherwise mostly insectivorous. Many species in this group are part-migrants with some warblers, such as the Garden Warbler, even long-distance migrants.

**Carnivorous species**

In nature the top trophic level is represented by the carnivorous species. Birds of prey, including falcons and owls, which prey on mammals and other birds, find food throughout the year. Many of them are resident birds. Only the populations in Northern and Eastern Europe suffer from a shortage of food in winter and these therefore migrate, in part, to climatically more favourable areas in Central and Southern Europe as well as to Asia. Insectivorous falcons, such as the Hobby and the Lesser Kestrel that do not find adequate food in our climes in winter, are characteristic migrant species and winter in Africa.

Exceptions to the rule are harriers, kites, and several eagle species that theoretically could also find food in winter in Europe. They are however, all migratory species, probably because the ancestors of these birds of prey evolved in tropical Africa.

Piscivorous marine bird species (petrels and shearwaters, gannets and auks) are frequently colony breeders that undertake long journeys across the oceans after the breeding period to find the best fishing grounds. Whereas gulls are normally resident or long-distance foragers, migratory behaviour is very pronounced in terns and some species, such as the Arctic Tern, belong to the exceptionally long-distance migratory species.

**Insectivores**

Insectivores, or more correctly arthropod-eaters, belong formally to the carnivorous species, but should be considered separately. In Central and Northern Europe, insects occur in large numbers only in late spring and summer. Many insects die in autumn, or winter in sheltered places where a ‘normal’ insectivore (unless it is a woodpecker, tit, or tree-creeper) cannot feed on them. The insectivores include a particularly large group of long-distance migratory species that winter south of the Sahara. In this category are the Corncrake, Coraciiformes (Hoopoe, Bee-eater, Roller), cuckoos, nightjars, swifts, Wryneck, swallows, pipits, wagtails, flycatchers, many different warbler species, small thrush species, wheatears, shrikes, Golden Oriole, and Ortolan Bunting.

Some insectivores are quite opportunistic, and species such as Chiffchaff, Blackcap, Dunnock, Pied Wagtail, Stonechat, and Firecrest, are short-distance migrants from Central Europe into the warmer Mediterranean region. It can be speculated that these species previously lived on the Iberian Peninsula, which was not covered by steppe-tundra during the last ice age. Only a few specialist insectivores, such as the Winter Wren, Goldcrest, and Dipper winter here in Central Europe. These are comparatively small species, whose dietary requirements are not as great as, for instance, a Hoopoe.

The question as to why one species migrates as a long-distance migrant to sub-Sahara Africa, and another remains resident or is a short-distance migrant only to the Mediterranean area, can be discussed on several levels:

- Climate and habitat change in the Pleistocene and Holocene
- The phylogenetic status of a species in the framework of phylogeny as a whole

Essentially the trend can be identified that bird species always become migratory when they cannot find food in their breeding area the whole year round. This applies at least to the present day, some 12,000 years after the end of the last ice age. It can be assumed that more than 12,000 year ago all species that we now know also existed then, as phylogenetic DNA analyses have dem-

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![The Bee-eater is a long-distance migrant that breeds in the warmer parts of Europe, North Africa, and western Asia (yellow) and winters in Africa south of the Sahara (blue).](Photo: M. Wink)
Glossary

Holocene - the geological epoch which began at the end of the Pleistocene (at 11,700 calendar years BP) and continues to the present.

Miocene - the first geological epoch of the Neogene Period and extends from about 23 to 5.3 million years ago.

Phylogeny - the history of the evolution of a species, genus, or family etc. Based on their evolutionary origin species are divided into monophyletic taxon, within which all the members have a common ancestor.

Pleistocene - the geological epoch which lasted from about 2.5 million to 11,000 years ago, spanning the world’s recent period of repeated glaciations.

Pliocene - the period in the geologic timescale that extends from 5.3 to 2.5 million years before present.

On the migration routes of birds. Bird migration

To begin with, the Sahara was a green savannah that did not have to be crossed in non-stop flight, but rather in stages. As the Sahara again reverted to desert some 6,000 years ago many species evidently developed the non-stop flight crossing. But even today there is still evidence that a number of species make short stopovers during their crossing of the Sahara, as did their forebears for thousands of years when the Sahara was still green.

If the typical long-distance migrants such as Hoopoe, Bee-eater, Roller, cuckoos, nightjars, swifts, Wryneck, swallows, pipits, wagtails, flycatchers, many different warbler species, small thrush species, wheatears, shrikes, Golden Oriole, and Ortolan Bunting are considered, these are all species whose genus has other representatives in Africa (some in South-east Asia as well) that did not evolve into long-distance migrants. The evolutionary motto for many migratory birds that visit us in the summer half-year (as it is for modern man who emigrated from Africa some 90,000 years ago) is therefore “out of Africa”. Where molecular family trees are available (i.e. for swifts, Acrocephalus, Hippolais and Locustella warblers. Wheatears, Stonechats and Whinchat species, and swallows) it can be clearly perceived that the European representatives of these groups are descended from African ancestors.

The trait ‘migrant’ is clearly genetically determined, such that ‘zugunruhe’, migratory behaviour and direction, and the locations of summer and winter quarters, all exhibit inherited components. The genetic traits are evidently flexible, as it has been proven that some bird species can alter their migration behaviour over the course of only a few generations (e.g. White Stork, Blackcap). This flexibility was probably necessary in the course of evolution as Europe was probably settled “out of Africa” several times in the past periods of climate warming. Today, we cannot determine whether or not the same species became migratory birds in these cycles. The European birds’ life in previous warm periods probably looked very different than it does today. As most of our species originated at least one million years ago, they have successfully mastered climatic changes (otherwise they would have become extinct). This flexibility can help us to be optimistic about whether and how our bird world will cope in future with the climate changes forecast by climatologists (see pp. 58–61).

It would seem that both migration in birds and the distribution of species are subject to constant adaption to changing circumstances. If we assume that learned information cannot be passed on, changes in bird habits must be the result of the elimination of those that fail to adapt. As Heraclitus would have put it – everything flows!

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