Each year, thousands of millions of African birds undertake seasonal movements, ranging from a few hundred kilometres to epic trans-continental journeys of more than 10 000 kilometres.

Of the approximately 1 800 bird species found in sub-Saharan Africa, nearly 200 species migrate seasonally between the Palearctic (Europe and Asia) and Afrotropical (sub-Saharan Africa) regions. A further 50 or so migrate between Africa and the New World, Antarctica and oceanic islands. In addition to these, more than 580 species are known to undertake seasonal migrations within the continent.
There is no common thread linking the migratory bird species of Africa. They are almost as diverse as the resident species, representing nearly all of the 21 Orders of birds found on the continent. Migrants are as different from one another as seabirds from owls, wanderers from rats and storks from warblers, to name a few. There is nothing that makes migratory species stand out from their non-migratory counterparts — they generally do not show any morphological adaptations for migration in comparison to closely related resident species. Even body size appears to form no barrier: African migrants range in size from the nine kilogram Dalmatian Pelican Pelecanus crispus to warblers less than one thousandth of that size.

**Why migrate?**

The high proportion of species and the sheer numbers of birds that migrate annually bear testimony to the success of migration as a life history ‘strategy’ for birds. Seasonal migrants benefit by moving between environments where breeding is successful and environments where survival during the non-breeding season is relatively easy. Species which occupy environmentally stable habitats, such as equatorial rainforests, tend to be sedentary because of a fairly constant year-round supply of food. Those occupying habitats which undergo marked seasonal changes in environmental conditions are more likely to be migratory. Species which have ‘opted’ for a migratory way of life generally take advantage of the relatively high summer productivity in strongly seasonal habitats, either just for breeding or, in the case of trans-equatorial migrants, for both the breeding and non-breeding seasons. Migration allows them to occupy high-quality breeding habitats that would not be able to sustain them adequately (if at all) during the rest of the year.

The extreme mobility of birds in Africa raises questions about the seasonal changes in community composition, particularly with regard to competition for food resources between migrants and residents, and amongst the migrants themselves. Although very little research has assessed competition between residents and migrants, a simple explanation may be presented as follows. The number of resident birds that any seasonal habitat can support will be determined by the conditions during the worst part of the year. Some of the increased food production during the breeding season (when conditions are best) will be required to satisfy the increased food demand of birds during this period, but the more seasonal the habitat, the more likely there will be a surplus of food even beyond these requirements.

**How do migrant birds find their way?**

Much of migratory behaviour is inherited genetically. Although the majority of newly-hatched juveniles set off on migration in family parties or in flocks with adults, the juveniles of many species, particularly those breeding in the Arctic regions, depart without (usually later than) their parents. The youngsters will have inherited a complex programme which guides them through their first migration experience, during which they develop and expand their ‘familiar area’.

Experimental evidence suggests that, on the programmed date, birds set off on migration, following a programmed red direction for a programmed length of time. The timing of migration is triggered by the aid of the bird’s ‘circannual clock’, and is probably also linked to changing day length and in some cases, climatic cues. Once the time is right, other factors (such as the size of the gathering flock, wind speed and time of day) then determine the moment of departure.

Although gradually progressing along their programmed path, juvenile birds actually make a lot of exploratory movements, rather than sticking to a narrow, uni-directional path. To maintain their programmed general direction, the young birds are usually able to orientate (as opposed to navigate). Birds have been shown to be able to orientate using several different compasses, including the sun, stars, and the earth’s magnetic field. From polarized light is used to ascertain the sun’s position in cloudy conditions. By orienting according to its genetic map, the juvenile migrant will arrive in the general area of its non-breeding grounds, and may then have to search for an appropriate site to spend the winter.

During their first migratory journey, the juvenile birds integrate the topographical, celestial, meteorological and magnetic cues perceived along the way to form a complex spatial memory of their familiar area. Thus, once a bird has completed its first round trip, it will have learned enough to be able to navigate (rather than simply orientate), to and from the non-breeding grounds in subsequent years.

This surplus provides a niche for migrant visitors. In equatorial forest areas where rainfall and food supply are more constant, this surplus is likely to be negligible, which would explain why relatively few migrants visit these habitats. In addition to this ‘surplus niche’, many non-breeding migrants occupy marginal habitats which cannot support resident birds throughout the year. Although there is undoubtedly competition between migrant species themselves, there are areas in which this is somewhat alleviated by different species occupying the same areas at different times of year.

**Patterns of migration**

Although several broad patterns of migration can be recognized among African bird species, such as the well-known Paleartic-Afrotropical ‘flyways’, there is almost as much variation within these patterns as there are migrant species. Regular seasonal movements by birds have almost certainly occurred for as long as birds have been mobile, but many of the patterns we see today are probably fairly recent: migratory patterns as there are migrant species.

Broader scale intra-African migration patterns are largely governed by the wet and dry periods associated with the

**Left** Abdim’s Stork is one of the more common intra-African migrants. The White Stork (right), however, is a trans-continental migrant and, like many other migratory species which share its plight, is dependent for its survival on the implementation of effective conservation measures which can only come about through improved knowledge of their ecology and movements and through international co-operation.
seasonal movements of the Inter-tropical Convergence Zone (ITCZ). In July, the ITCZ, essentially a low-pressure belt, lies in a fairly straight line along the northern Tropic of Cancer. By January the ITCZ lies in a more uneven configuration from the equator in the west, dipping southwards to Zimbabwe in the south and turning northwards again to Tanzania. The oscillation of the ITCZ between these two extreme positions results in a corresponding movement of rainy weather, from the northern hemisphere in the northern summer to the southern hemisphere in the southern summer and back again. As a result, most of Africa experiences a summer rainy season, with the exception of East Africa, which experiences two wet seasons every year as the ITCZ passes to the north and south, and the winter-rainfall regions of the southwest Cape and parts of North Africa.

Most intra-African migration systems are closely related to the alternation of rainy and dry seasons which results in sudden and far more dramatic changes of weather than, for example, the gradual transition of winter to spring in more temperate latitudes. The onset of the rainy season is often highly predictable and usually quite dramatic, resulting in a proliferation of plant and animal life. Insects are most abundant early in the rains, which also see the emergence of magnificent termite swarms. Although most migrants take advantage of the increased productivity of the wet seasons, there are a number of species, notably raptors, that prefer drier conditions and migrate away when the rains come.

A large number of intra-African migrants cross the equator to take advantage of seasonal rains and food abundance during both their breeding and non-breeding seasons. These trans-equatorial migrants include northerly breeders such as Abdim’s Storks Ciconia abdimii and southerly breeders such as Lesser Striped Swallows Hirundo abyssinica.

Many more species migrate between the northern or southern parts of the continent and equatorial regions. Hordes of tropical migrants such as herons, cuckingeet-eaters, kingfishers, nightjars, flycatchers, weavers and sunbirds follow the rains northwards from the tropics to the Sahara or Sahel, some migrating there to breed, and others to spend the non-breeding season. Many species which breed in southern Africa during summer, including cuckoos, bee-eaters, swifts, flycatchers and owls, migrate northwards during autumn. Wahlberg’s Eagle Aquila wahlbergi, on the other hand, breeds in southern Africa during the winter dry season and moves northwards during the wet season. Some species, like one of our better known harbingers of spring, the Redheaded Cuckoo Cuculus silvanus, breed in both northern and southern Africa and converge to spend the non-breeding season in the tropics.

In many cases where a species’ breeding range extends from the tropics to the temperate areas, those individuals which breed away from the tropics migrate to the tropics and those breeding closer to the tropics are resident there. In other words, individuals that occupy breeding grounds which are closer to benign non-breeding areas tend to be less migratory, resulting in the phenomenon of ‘partial migration’.

Probably the most impressive and well documented of the migratory pathways are those which converge from the Palearctic regions into Africa along a handful of narrow passages across the Mediterranean, crossing formidable tracts of sea and desert. Many African bird species migrate to breeding grounds in the tundra areas of the far north and eastern Eurasia. Here, the breeding season is concentrated into a short spring and summer when there is a proliferation of life, insects in particular, and breeding conditions are ideal. There is no loaﬁng around however, as these conditions are short-lived: the advancing cold weather and impending food shortages soon compel birds to head south.

Palaeartic–African migrants follow a variety of migratory routes, but their diversity decreases steadily towards the south with about half the number of species reaching South Africa.

Superimposed on the above patterns of intra-African and intercontinental migration is the phenomenon of ‘leap-frog migration’. This is particularly well illustrated among some of the longer distance migrants, in which birds breeding in Arctic regions overﬂy the breeding and non-breeding grounds of their counterparts that breed further south. In fact, among African migratory shorebirds, two distinct groups of species can be recognized: short-distance migrants which breed in mid- to low north-temperate latitudes and winter north of the equator, and broad-ranging migrants which breed from north-temperate to high Arctic latitudes and winter over a range from low north-temperate to south-temperate latitudes, effectively leap-frogging the short-distance migrant species.

Many insectivorous species undertake what is known as ‘step migration’, stopping in North or West Africa for two to three months to take advantage of the rainy season until about November, before moving on to the southern hemisphere summer. Other species simply stop at sites for as long as it takes to rest and regain the energy required to complete the next stage of the journey.
CONSERVATION OF MIGRANTS

One of the greatest threats to migrants worldwide is habitat loss. Isolated wetland habitats, upon which millions of shorebirds and waders rely, are succumbing in rapid succession to development projects, and savanna and grassland habitats are increasingly over-grazed and transformed.

The conservation of migrant species is much more complex than that of sedentary species. Migrant populations must be conserved on both their breeding and non-breeding grounds, as well as at important staging sites, by means of carefully designed reserve networks. Apart from the necessary international co-operation, achieving this ideal requires a detailed understanding of the movements of bird populations.

The survival of many migrant species is further threatened by hunting. Of the five billion migrants that cross the Mediterranean on their way to and from Africa, it is estimated that somewhere in the order of a fifth – some one billion birds – are killed annually by hunters, for food, and increasingly, for sport. Almost all types of migrants fall prey to shotguns, nets and traps in these countries, giving rise to a different set of priorities.

Hunting is more powerful than the conservation lobby in several countries, this directive is frequently ignored.

There are a surprising number of organisations and legal agreements dealing with the problems of migrants and their conservation, particularly in Europe, yet the future of many migrant species appears to be bleak. Existing programmes are mostly insufficient, because they lack co-ordination, and the contracting parties have not become as aware of the importance of these areas as they need to be. The global economic pressure on the co-operation of developing countries in Africa to protect vital parts of migrants’ ranges, but burgeoning population growth in these countries gives rise to a different set of priorities.

Conservation of Migrants

Migrants may traverse the continent in short ‘hops’, longer ‘skips’, or impressive, long-distance ‘jumps’. Although it is the latter movements that really capture the imagination, most African migrants probably opt for relatively short-distance movements. This is because a great many species are able to stop and feed as they go. These birds replenish their energy reserves on a daily basis, and may migrate for only a few hours, covering less than 200–300 kilometres each day. This strategy is also shared by some larger birds, such as Steppe Buzzards Buteo bubo, which stop regularly to hunt for prey. In some cases the lengths of flights are restricted for other practical reasons – large birds such as storks, which rely on warm thermals to glide, may only be able to fly for a few hours during the day.

Species which migrate long distances between stopovers tend to be those for which feeding en route is more difficult. The long nocturnal flights of shorebirds, for example, may be necessitated largely by a scarcity of suitable wetland habitats. Shorebirds have been known to accomplish some fantastic distances in short periods: one Turnstone Arenaria interpreps, captured four days after it was ringed, had travelled 3 650 kilometres, while another, recovered 14 days after being ringed, had covered some 7 000 kilometres.

The distances of their non-stop flights are reflected in how different long-distance migrants prepare for migration. The majority of migrants, which usually travel short distances between stopovers, feed and travel the distance more readily. However, many of these species are capable of increasing their weight significantly, and so do by up to 30 or 40 per cent immediately before crossing the Sahara. In southern Africa, Palearctic shorebirds spend at least a month fattening up on their non-breeding grounds before migration. Small bird species are capable of doubling their body weight, but larger species must compromise between the size of their fuel reserves and their body mass to wing-area ratio and cannot lay down proportionally such large reserves. Most of the largest migratory birds are therefore heavily reliant on using energy-saving gliding flight. The extra weight is in the form of both increased muscle mass and fat used for fuel.

The journey back to the breeding grounds, which commonly follows a quite different route from the outward migration, is usually far more rapid than the outgoing migration, making a speedy return is necessary to ensure timely arrival on their breeding grounds, where they must compete for breeding territories and mates.

Migrating long distances between breeding and non-breeding grounds has interesting repercussions on the migratory strategies of young birds. The juveniles of many of the longer distance migrants often do not return to the breeding grounds in their first, and sometimes second year. This delay is probably an adaptive response to a low probability of breeding successfully, coupled with the fact that the risk of making a long-distance journey exceeds the benefits of staying behind. This is further exacerbated by the fact that the risk of getting lost or dying on migration is higher for young birds than for adults. Most of the ‘vagrant’ birds that are found at great distances from their usual migratory ranges are juveniles, and the probability of a juvenile long-distance migrant surviving its first year is thought to be as low as 30 per cent. The juveniles of shorter distance migrants, even within the same species, are more inclined to develop breeding plumage and migrate to the breeding grounds than those which have travelled to more distant non-breeding grounds.

Wahlberg’s Eagle migrates to summer breeding quarters, which extend from southern to East Africa. The exact whereabouts of its non-breeding grounds are now being discovered by means of radio-tracking.

The Consequences of Migrating Different Distances

Even in the context of all the patterns described above it is still noteworthy that some individuals of the same species migrate thousands of kilometres further than others. In many species one sex migrates further south than the other. In nearly all cases it is the sex which establishes the breeding territory that stays closest to the breeding grounds, and in species which lack strong sexual dominance there is less tendency for spatial separation of the sexes on the non-breeding grounds. Even so, some would argue that the longest distance migrants within homogenous groups are subordinate birds which are forced to migrate further due to competition for non-breeding sites closer to the breeding grounds.

The most likely explanation lies in a trade-off between the risk of dying on the non-breeding grounds and the risk of dying on migration. Grey Plovers Pluvialis squatarola which migrate from their Siberian breeding grounds to western Europe may suffer low mortality during their relatively short flight, but frequently encounter harsh weather conditions on these non-breeding areas when the risk of starvation becomes high. Those which survive the long and risky migration to the tropics and southern hemisphere, on the other hand, encounter comparatively stable climatic conditions. Those that travel the furthest to the south-temperate regions are further advantaged by the fact that their stay coincides with the summer season of high productivity of their invertebrate prey. Evidence suggests that the risk of predation by raptors also decreases towards the south. The different distance migrants are probably equally well-adapted in the long run, merely differing as to whether they risk their lives on the more northerly non-breeding grounds or continuing migration.