Avian Survivors

The History and Biogeography of Palearctic Birds

CLIVE FINLAYSON

AVIAN SURVIVORS

This page intentionally left blank

AVIAN SURVIVORS

THE HISTORY AND BIOGEOGRAPHY
OF PALEARCTIC BIRDS

CLIVE FINLAYSON

To my son Stewart,
gifted with the ability to feel the spirit of the wild

This book is produced using paper that is made from wood grown in managed sustainable forests. It is natural, renewable and recyclable. The logging and manufacturing processes conform to the environmental regulations of the country of origin.

Cover art by Tim Worfolk

Front: Gorham's Cave, Gibraltar, 40,000 years ago. Several miles inland, the cave lay above a plain of scrub not dissimilar to the Coto Doñana today, with Crag Martins roosting in the cave, Azure-winged Magpies foraging from bush to bush and Lammergeiers soaring above.

Back: Gorham's Cave today. Crag Martins still roost in the cave in good numbers, but the plain has been submerged beneath the sea for millennia.

Visit www.poyserbooks.com to find out more about our authors and their books.
You will find extracts, author interviews and our blog, and you can sign up for newsletters to be the first to hear about our latest releases and special offers

Contents

This page intentionally left blank

Preface

This book owes its existence to a man and to a bird. Both influenced me at key moments of my life and in fundamental ways that shaped my thoughts about the distribution of birds in the Palearctic and beyond: why is one species here and not somewhere else? Why are there more species in one family than in another? How do similar species manage to live side by side without one ousting the other? Why do some birds migrate long distances while others hardly move from the territory in which they were born? These questions are not new, and there is a huge body of ecological and ornithological literature that has tried to answer them, with varying degrees of success. Ian Newton's recent volumes (Newton 2003, 2008) provide excellent summaries of the literature as it applies to birds. So this book is not another synthesis of what has been written. It is, instead, a new approach that owes its origins to the inspirational works of the late Reg Moreau, the man I alluded to in the first sentence of this book.

I became familiar with Moreau's work very early in my career, as an undergraduate in 1973. His seminal book *The Palaearctic-African Bird Migration Systems*, published posthumously in 1972, was the culmination of years of field work, research and papers in journals such as the *Ibis*. It was, in the words of David Lack, 'his best work', and it is still the best ornithological book that I have ever read, and the one that has the central place in my library. I recommend it to everyone interested in bird migration for its clarity, insight, and as a limitless source for reflection. And it is also a fine example of how to write science in a clear, concise and engaging way.

Moreau's work was a catalyst to me. He raised my childhood passion for birds and migration to a new level, and I have not recovered from it since. My research path has taken me in many different directions in the intervening thirty-seven years, but I always end up leafing excitedly through the pages of his final work as though it was the first time. I ask for forgiveness from readers for submitting them now to a brief history of my own career but I feel it is essential, not out of vanity or self-importance, but because it provides an explanation for the reasons why I have written this book.

I grew up close to birds; the phenomenon of bird migration was ever-present, as I watched the annual movements of all kinds of birds crossing the Strait of Gibraltar between Europe and Africa, just as the Reverend John White, Gilbert White of Selborne's brother, had done in the same spot two hundred years before (White, 1789). Bird migration stimulated my interest in nature and pointed me in the direction of zoology as a subject of study. On completion of my zoology degree at the University of Liverpool I was lucky to be awarded the first David Lack studentship by the British Ornithologists' Union and, in 1976, I went to read for a DPhil at the Edward Grey Institute of Field Ornithology of the University of Oxford. Here I was to study the ecology of closely related species, attempting to answer the question of how two or more similar species could co-exist in the same area without one outcompeting the other. It was a natural consequence of David Lack's work on competition and his 1971 book *Ecological Isolation in Birds*. And it was also natural that the subjects of study should be swifts; after all, David Lack had dedicated much time to the study of the Common Swift *Apus apus* in the tower of the University's Natural History Museum (Lack, 1956).

As I was familiar with the swifts in Gibraltar, where I was born and grew up, it followed that this should be the place of study and I would compare two similar species – the Common Swift with the Pallid Swift *A. pallidus*. Unhappy with this species pair alone, I decided to add a comparison of two *Sylvia* warblers that also nested in Gibraltar – Sardinian Warbler *Sylvia melanocephala* and Blackcap *S. atricapilla*. This was an interesting combination as these Blackcaps were quite unlike their northern counterparts – dull with short, rounded wings, they lived in the Olive maquis scrub and not in forest, and they shared space with Sardinian Warblers, the archetypal Mediterranean scrub warbler. My results revealed differences in food, behaviour

and life cycle in each of the two pairs but I was never happy that I had resolved the questions that I had set out to answer. I had found differences but the real question was whether or not these differences mattered – were they of a scale that allowed the species pairs to coexist?

These were the days before the personal computer, so complicated multivariate statistical analyses required the negotiation of computer time, and the results came out in lengthy printouts that needed acres of space to read and hours of peace to assimilate. Oh, what I would have given for a Windows-based package and a laptop then! But even the results, using the latest available analyses, simply explained proportions of the observed variation and left a lot to future interpretation or to dismissal as noise. The acid test of interspecific competition, to put two species in a controlled environment and alter variables one by one, might have worked for the Russian scientist Georgyi Frantsevitch Gause and his tiny protozoans in 1934, but could you even begin to think of replicating his experiments with swifts?

But my biggest misconception, and one that I should have expected had I read Moreau more carefully, was to think that I could explain everything that I saw without reference to history. And I was not alone in this. Ecologists looked at the present and thought that they could explain it in splendid isolation or, at least, even if history was acknowledged it was not that important or easy to submit to the scrutiny of statistics. So, for better or worse, I came away thinking that I had some kind of handle on what was going on between Common and Pallid Swifts and why they could live side-by-side. It would be another two decades before the penny would start to drop.

History is full of contingent events that matter and they happen at many scales, affecting individuals at one end and, less often, species at the other. The extinction of the dinosaurs at the Cretaceous-Tertiary (K/T) boundary is an extreme example of historical contingency affecting an entire lineage. Contingent events also shape and steer people's lives, and one such occasion manoeuvred mine in a new direction. It was in 1989 that I first met Chris Stringer and Andy Currant, palaeontologists at the Natural History Museum in London, who were visiting Gibraltar prospecting for cave sites that had shown evidence of occupation by Neanderthals when excavated in the 1950s. I got involved with them, fortuitously, because they wanted to see these caves, which were on military land, and I knew them well because I used to ring hundreds of Crag Martins *Ptyonoprogne rupestris* there every winter, when more than 3,000 birds used the caves to roost. Little did I know then that beneath the sandy slopes by the cave entrances on which I placed my mist nets were rich archaeological and palaeontological deposits going back to the time of the Neanderthals.

This was the start of my involvement with the world of the remote past. I need to impose on the reader's patience a little longer by describing this world of caves and bones, because it gives some kind of context to the words that will compose this book. Often at the end of a day of excavation inside Gorham's Cave, the main site that we have been working in Gibraltar for over two decades now, I would stand at the cave entrance and let my colleagues go ahead. Once on my own I would stare at the dark Mediterranean Sea and feel the past. I would be standing on eighteen metres of sediment accumulated over the past 60,000 years. In the sediment were the bones of countless birds, mammals, amphibians, reptiles and fish that had lived and died in this remote place. There were dark patches that marked old Neanderthal camp fires and the charcoal told us which plants had been growing outside the cave, and when they had done so. There were limpet and mussel shells that had been collected from the beach by Neanderthals. And I knew that there were also, invisible to the eye, millions of pollen grains that spoke to us about the vegetation of a distant past.

Imagine my excitement all those years ago when I found my first Crag Martin bones in a context that associated them with 40,000-year-old Neanderthals in Gorham's Cave, the same cave where I had been ringing them for years. The martins had been there all the time. We have now identified the remains of 145 bird species in a small group of caves and rock shelters on the eastern side of Gibraltar. Put into some kind of context, that represents 26% of the Western Palearctic breeding species that we will be looking at in this book in a mere 6-kilometre stretch of coast. But it is a stretch that contains a unique 300,000-year-old archive. Here we had a wealth of information about the birds of today and what they had done yesterday, and that got me straying more and more, while I discussed the Neanderthals with my colleagues in the cave,

into the world of the Pleistocene. This had also been Moreau's world, as he had clearly seen and recognised that we ignored past climate and vegetation change at our peril.

Having introduced the man, it is now time to bring in the bird. It is the Iberian Azure-winged Magpie *Cyanopica cooki.* When I started off in science, this bird was considered conspecific with the Eastern Azure-winged Magpie *C. cyanus,* and it was one of those birds with an unusually disjunct distribution. It occurs in south-western Iberia (but curiously not in Gibraltar – the significance of this parenthesis will become apparent in a moment) and in the Far East, in parts of China, Japan and Korea. It seemed an impossible exemplar of natural range fragmentation, and the popular view for years was that these colourful birds had been brought back from China by Portuguese mariners in the late medieval period and then escaped, going feral, in south-western Iberia (Finlayson 2007). Azure-winged Magpies were in some distant way part of Marco Polo's legacy.

Then, during our excavations, the remains of these magpies were found in Gorham's and Vanguard Caves, in contexts dating back well into the Pleistocene, to 40,000 years ago and beyond (Cooper 2000). This discovery altered everything. The magpies were native to the south-west of Europe and had not been introduced by humans. That simple observation changed the way in which I viewed the Palearctic and its birds. My first reaction was to try and understand, at the local level, how it was that Azure-winged Magpies had lived in Gibraltar and did not do so now (my parenthesis above should now become relevant).

That question took a little while to answer and it was resolved in collaboration with my wife Geraldine, who was studying the past landscapes outside Gorham's Cave, and my good friend Pepe Carrión from the University of Murcia who was looking at the pollen samples. The answer went something like this. The deep blue Mediterranean that I would stare at from the cave was today in an unusually high position, lapping the beach immediately below the cave. For the greater part of the Late Pleistocene, global temperatures had been lower that today and, as water became trapped as ice at the poles, sea levels dropped. The submerged shelf outside our cave was shallow and we calculated that at times the coast had been as much as 4.5 kilometres away. In fact, for most of the past 100,000 years sea level had averaged around 80 metres below present levels, and it had been as much as 120 metres lower (Finlayson, 2009). Here we had a vivid image of the scale of past natural climate change and its impact on the landscape. I sometimes take people to the cave by boat and we sail out until we are 4.5 kilometres from the cave, at which point I surprise my visitors by telling them that the whole stretch of sea that we have sailed across was once the hunting ground of Neanderthals, Spotted Hyenas and Leopards.

It was indeed a rich landscape between 50,000 and 28,000 years ago, dominated by herds of grazing animals, especially Red Deer *Cervus elaphus*, wild horse *Equus ferus* and aurochs (wild cattle) *Bos primigenius*. It had a suite of predators, and also scavengers; Bearded Vultures *Gypaetus barbatus* nested on Gibraltar's cliffs, which were practically at sea level (a lesson for those who see the relictual few as having some kind of montane fixation), and there were lots of Red Kites *Milvus milvus,* Egyptian Vultures *Neophron percnopterus* and Griffon Vultures *Gyps fulvus,* with a few Black Vultures *Aegypius monachus* thrown in. It was a Mediterranean Serengeti, a vast complex of savannas and wetlands on sand. And the tree that grew preferentially on this sand, as it does today in the coastal National Park of Doñana in south-west Spain, was the Stone Pine *Pinus pinea*. If there was to be a third character in my story it would be this tree, because of its close association with the Azure-winged Magpie.

Go to Doñana today, a mere 125 kilometres from Gibraltar as the magpie flies, and you will find lots of Azure-winged Magpies on Stone Pine savannas. The rising sea over the last 10,000 years flooded the pine savannas off Gibraltar; there are no magpies there now. But go back to the Late Pleistocene and you will find a land of stone pines and magpies, right outside Gorham's Cave. By contrast, at this time there is nothing at Doñana but open ocean – the sand spit that would close the coast off and create the dunes for the pines and the magpies would only form some time after the Romans had arrived in Iberia, with Doñana's marsh the product of silting caused by deforestation upriver as men cut trees to make invincible armadas. Spain's emblematic national park has a recent origin, and has been largely shaped by the hand of humanity.

So this answered the first question. Azure-winged Magpies, Stone Pines, dunes and coasts had been in constant flux within the local context of south-western Iberia. There is another point that I want to make before moving up a scale with our magpies. When I started all this work another prevalent misconception was that Stone Pines were somehow unnatural. In most contexts they were planted and we had somehow helped them along. But now we know that this is not true. We have planted many forests of Stone Pine, but these trees have been growing on the coastal dunes of this part of the world for a very long time, as the evidence from Gorham's Cave has shown.

There seems to have been an obsession with regarding the potential natural vegetation of the Iberian Peninsula as somehow dominated by oak forests, which we have later cut down. But it has once again been Pepe Carrión who has bravely begun to take on long-established and firmly entrenched positions. He has ably demonstrated, using a wealth of pollen data from across the Iberian Peninsula, that the natural vegetation over much of this land was dominated by various species of pine (Carrión and Fernández 2009). Results such as this one also have a major impact on how we understand the history of the birds of the Palearctic.

I started to delve deeper into the Azure-winged Magpie's message to us as far back as 2000. I realised then that there must have been, at some point in the remote past and very likely long before the Pleistocene glaciations, suitable habitat for Azure-winged Magpies all the way from Portugal to Japan. I had been trying to understand the wider picture of Neanderthal distribution, and I was convinced that the belt of mountains that stretched from Iberia to China had provided a continuum of topographically varied landscapes that had been the mainstay of the Neanderthal economy. I called this belt the heterogeneous mid-latitudes (Finlayson *et al.* 2000) and later (Finlayson 2004) the mid-latitude belt (Figure 2.3, p. 28). I also introduced the southern ranges, from the Arabian Peninsula south down the Rift Valley to South Africa, as an extension of this belt that crossed latitude lines. When I started to look at birds I realised that many followed a similar pattern of distribution – Bearded Vulture, wheatears, rock thrushes and choughs, for example – but these were not limited to birds of rocky habitats. I found similar patterns for wetland birds and for birds of savannas (by which I mean the gamut of habitats with trees at densities low enough not to be forest). The Azure-winged Magpie was the smoking gun. I presented my preliminary results at a conference that I hosted in Gibraltar in 2007; Jacques Blondel, another of those legendary ornithologists whose writings influenced me unmeasurably, listened to what I had to say and encouraged me to publish. He was, incidentally, one of the few people who had tackled the history of the avifauna of the Western Palearctic (Blondel and Mourer-Chauviré 1998) and had a clear vision of the role of history in its formation (Blondel and Vigne 1993). I decided, after much deliberation, that a short paper would not do justice to the results. I needed to verify my data, add to them and then think of publishing them as a book. And this is it!

There are two epilogues to this introduction and they both matter because they had a major influence on my thinking. The first is that, following the publication of the discovery of the Azure-winged Magpie fossils, interest in these birds gathered momentum and two papers were published that compared the DNA of eastern and western magpies (Fok *et al.* 2002; Kryukov *et al.* 2004). Most interesting were the estimates for the split between the two populations, admittedly broad given uncertainties about mitochondrial clock calibration – anything between 3.35 and 1.04 million years ago. This placed the split either in the Early Pleistocene or, more likely in my opinion, the Pliocene.

The second epilogue comes from the world of human evolution that I had also kept up with and had been writing about. A paper appeared in the journal *Nature* at the end of 2005 in which archaeologists Robin Dennell and Wil Roebroeks argued that a corridor of savannas, across which our early ancestors had dispersed, had stretched from Portugal to China during the Pliocene. They called it 'savannahstan' (Dennell and Roebroeks 2005; Dennell 2009). It seemed that we were independently coming to similar conclusions. When, in 2009, I presented my improved dataset at the Calpe 2009 Conference, Robin Dennell was in the audience. His lecture at the conference added to his earlier paper and we shared one of those indescribably stimulating moments of intellectual convergence.

Acknowledgements

This page intentionally left blank

CHAPTER 1
Introducing the Tertiary

Sometimes, on rare occasions, a piece of information is revealed that opens up a window of opportunity for a new understanding of data that we may have been unimaginatively staring at for years. This revelation may come through personal inspiration, perhaps while in the field, or it may be an insight gleaned from a new publication or even by looking afresh at an old one. A paper by John Klicka and Bob Zink of the Bell Museum of Natural History of the University of Minnesota, published in 1997 in the journal *Science,* was one such eye-opener. The paper's title said it all – *The importance of recent Ice Ages in speciation: A failed paradigm.*

This paper challenged the long-established view that the Pleistocene, particularly the Late Pleistocene during which time much of the Palearctic was engulfed in ice sheets, had been a period of speciation for vertebrates in general (Mayr, 1942, 1963; Simpson, 1944) and birds in particular (Mengel, 1964; Bermingham *et al.*, 1992). Klicka and Zink argued that most North American songbird lineages had instead had a protracted history of speciation over the past 5 million years (mya). These results have been contested by others (Johnson and Cicero, 2004; Weir and Schluter, 2004; Cicero and Johnson, 2006) and reinforced by the authors (Zink *et al.*, 2004), which would seem to leave the debate open to further discussion. Lovette (2005) has provided a balanced analysis of the situation; the most closely related sister taxa and lineages seem to have split during the Pleistocene, and there seems a bias in favour of such diversification among boreal over low-latitude species (following Weir and Schluter, 2004); but this is only the tail-end of a long history of lineage-branching; the majority of birds have had long tenures as independent lineages that pre-date the Pleistocene. Although the debate and analyses have focused on North American songbirds, the general conclusions are pertinent to the Palearctic.

A separate but equally significant debate concerns the origins of the main avian lineages, once thought to be the result of diversification after the K/T Event (the massive asteroid impact together with major volcanic activity and sea-level changes that was responsible for the mass extinction of dinosaurs and other animals at the end of the Cretaceous) of 65 mya. Clear evidence of a pre-impact diversification of mammals, going back as far as 170 mya, has emerged from fossil sites in China, Madagascar and Portugal (Hu *et al.*; 2005; Weil, 2005; Ji *et al.*, 2006), and it now seems that many lineages of present-day birds were already present in the Mid- to Late Cretaceous, and subsequently survived the K/T Event (Cooper and Penny, 1997; Cracraft, 2000; Clarke *et al.*, 2005; van Tuinen *et al.*, 2006; Brown *et al.*, 2008; Pratt *et al.*, 2009). Not everyone agrees and some still situate the avian radiation after the K/T event (Feduccia, 2003; Chubb, 2004; Poe and Chubb, 2004; Ericson *et al.*, 2006).

What is important to us here is that modern bird lineages have been around for a very long time, and their origins are ancient. Whether before or after 65 mya, these lineages have had a long history and have been exposed to the massive climatic and ecological changes of the Tertiary (65–2.6 mya; traditionally, the boundary between the Tertiary and the Quaternary was considered to lie at 1.8 mya, but a recent revision has placed it at 2.6 mya, within the older bracket of the Pliocene, the last epoch of the Tertiary) and Quaternary (which encompasses the Pleistocene and the Holocene, the latter representing the last 10,000 years of global warming). This means that the Tertiary represents, in terms of time taken, the equivalent of 24 Quaternary periods. The relatively short length and climatic variability of the Quaternary has not generated large-scale speciation, and has not seen the evolution of new genera of birds.

We have already seen (see p. 10) how the azure-winged magpie split pre-dated the glaciations of the

Middle and Late Pleistocene and had probably occurred during the Pliocene. This is a marker of a wider picture of events that may have been taking place throughout the Tertiary, and which may have gathered momentum during the Miocene (after 10 mya until 5.33 mya) and Pliocene (5.3–2.6 mya), for reasons that I will explain in this chapter. It is noteworthy that this was also the time during which significant evolution and radiation of the human lineage took place (Finlayson, 2009). Moreau's (1972) chapter on the fluctuating ecology of the Palearctic was limited to the Pleistocene. This is hardly surprising given the established view at the time regarding the importance of the Pleistocene and the lack of detailed information on earlier geological periods. But it is also an indication of his insight that he limited the discussion to the distribution and re-distribution of species and not to the formation of new species.

There are two possible biological responses of species to climate change: (a) their geographical ranges can shift, contract or expand, which is what Moreau (1972) was looking at; or (b) they can evolve by adapting to changing environments without moving and they can also, when isolated, branch off in different evolutionary directions and become different species. If the above fail then extinction will follow (Bennett, 1997). My basic argument in this

Figure 1.1 *Approximate time-line for the main geological periods described in this book, starting at the K/T boundary 65 million years ago. Numbers on the left of the column are millions of years. The major periods of the Tertiary and Quaternary are to the right of the column.*

book is that species have frequently responded to climate change by shifting geographical position to keep to their preferred ecological conditions. When these conditions have disappeared altogether, species have invariably become extinct. But when ecological change has been in a single direction and has been slow, gradual or has persisted for long periods, then species have had the chance to change and evolve with the new conditions. The climatic changes of the Pleistocene have been so severe and rapid away from the tropics that there has been little room for evolution and speciation, and redistribution has dominated. There is little evidence, as we will see, of large-scale avian extinctions in the Pleistocene either, which suggests that the species that made it to the Pleistocene were the 'survivors' that had the ability to withstand the oscillations of the climate of the last two million years. We will test this prediction in the chapters that follow. For the rest of this chapter I will summarise the main climatic and ecological changes of the Tertiary and Quaternary.

FROM THE PALAEOCENE TO THE
END OF THE OLIGOCENE (65–23 MYA)

This long span of time covering 42 million years is the backdrop to the latter part of the Tertiary that will be of greater interest to us. It marks the zenith of a 'hothouse' world that progressively drifted towards the 'icehouse' world in which we live. A rise in global temperatures at the start of this period (the Palaeocene, 65–55 mya) culminated in one of the warmest episodes in the Earth's history. Global tectonic events increased hydrothermal activity in the sea floor, flooding the atmosphere with carbon dioxide (CO_2) (Rea *et al.*, 1990; McElwain, 1998). Deep oceanic water temperatures were between 9° and 12°C warmer than

today, and the Antarctic Ocean's surface temperatures were of the order of 21°C (Kennett and Stott, 1991). The warming was rapid; global sea-surface temperatures rose by 8°C in 10,000 years.

During this time there was an intermittent connection between North America and Europe via Greenland, and as evergreen forests stretched across high latitudes of the northern hemisphere, the world witnessed the expansion of early tree-dwelling primates (Beard, 2008). The position of the continents influenced the situation. Africa and India were separated from Eurasia by the Tethys Ocean, and the Mediterranean Sea had not formed. Australia was still joined to Antarctica, which was connected via a series of islands to South America. Warm water was carried towards high latitudes, keeping a low-temperature latitudinal gradient and the poles ice-free.

The vegetation belts of Eurasia, Greenland and North America (or 'Holarctica') followed latitudinal bands with a limited amount of polar broadleaved deciduous forest in the extreme north, a broad belt of subtropical (broadleaf evergreen) woodland to its south (across what would today be Canada and northern Siberia) and paratropical (seasonally dry) forest occupying a band to the south (including much of today's United States, south-central Siberia and temperate Europe). To the south of this lay a broad belt of tropical forest covering the whole of Africa, Madagascar, India, southern Asia and southern Europe. There was also a block of ancient woody savanna on the early high ground of a very young Tibetan massif (Janis, 1993).

This Eocene thermal optimum would come to an end, leading to a steady downward trend in global temperatures to the present day; there have been many oscillations and temperature reversals along the way, of course, and not just during the Pleistocene (Bennett, 1997). But the world never saw temperatures of this magnitude again, and present-day predictions of human-generated global warming are minuscule in comparison. The main culprits of the downward temperature spiral (for there were several) were the Earth's land masses, which were gradually drifting toward their positions of today. In the process they altered the flow of ocean currents and air masses.

The most significant of these movements was probably the first major phase of uplift of the Tibetan Plateau, as India collided into Eurasia around 54 mya. Over the following 45 or so million years the plateau, an area roughly half that of the United States, was thrust five kilometres into the air, influencing atmospheric patterns, deflecting jet streams and intensifying the monsoon (Ruddiman and Kutzbach, 1991). As rainfall increased, larger amounts of atmospheric CO_2 were dissolved. The resulting reduction in atmospheric CO_2 reduced the greenhouse effect, and global temperatures subsequently decreased. Other geological events intensified the effect: there was massive volcanic activity on the North Atlantic seabed, two Antarctic marine gateways opened up (Drake Passage between Antarctica and South America and the Tasmanian Passage between Antarctica and Australia), the Andes and Rockies were elevated, and the Central American Seaway between North and South America began to close (Figure 1.2). All these factors contributed to the decrease in global temperatures and, because these events were irreversible, the trends continued in one direction – towards cooling.

The world of the Eocene hothouse is relevant because its birds included many kinds that would disappear from the Eurasian landmass as the tropical forests disappeared and climatic conditions cooled. There was undoubted global extinction of species and families, but there was also a significant degree of loss at the regional level. Many of these birds of tropical forests left lineages that are today only represented among the birds of the Neotropical, Afrotropical and Indo-Malayan regions. Among the fossils recovered from the Eocene and Oligocene of Eurasia (from sites such as the Messel Shales in Germany) are trogons (Mayr, 2005a, 2009), barbets (Mayr, 2005b), turacos (Musophagiformes), motmots (Momotoidea), hummingbirds (Trochilidae), mousebirds (Coliiformes; Mayr and Peters, 1998; Mayr, 2000; Mayr and Mourer-Chauviré, 2004), hornbill-types (Bucerotes; Mayr, 2006a), New World Vultures (Cathartidae), secretary birds (Sagittariidae) and parrots (Psittaciformes) (Mayr, 2005c). There are also taxa that became globally extinct, for example the swifts of the family Jungornithidae (Mayr, 2003) or the galliformes of the Gallinuloididae (Mayr, 2006b). This early contraction of range and loss of bird taxa was the first step towards the present configuration of the Palearctic avifauna.

Many of these groups, which are now missing from the Palearctic avifauna, are typified by an absence of migratory behaviour, while many extant Palearctic groups which have tropical representatives include
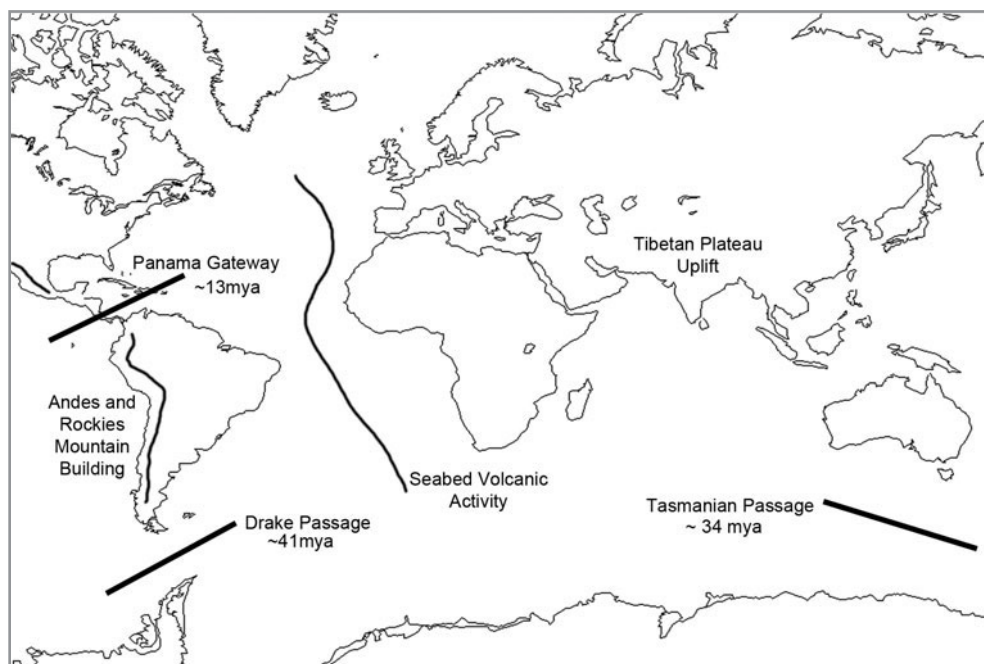
Figure 1.2 *Major tectonic events affecting Tertiary climate change superimposed on a present-day map. Dates for the opening of Tasmanian and Drake passages and closing of Panama are approximate and indicate the start of protracted processes. Mountain building similarly was protracted, with rates of uplift varying at different times during the Tertiary. For example, the uplift of Tibet started by 54 million years ago and activity continued to at least 7 million years ago.*

migratory species. It is impossible to disentangle whether migratory behaviour is missing from those absent from the Palearctic today simply because they live in situations that do not require migration or whether it is because they are *unable* to migrate. In the hot world of the Eocene, migration in the northern hemisphere's tropical forests may have been unnecessary; but there must have been limited, short-range migrations among birds of high latitudes that experienced annual cycles of long and short days, and those of the paratropical forests which had a dry winter season, just as there are intra-tropical, rainfall related migrations today (Moreau, 1966; Curry-Lindahl, 1981 a, b). These would have been the precursors of the long-distance migrations that characterise many Palearctic birds today.

Into the Oligocene

The Oligocene world, still considerably warmer than today's, was cooler than that of the preceding Eocene. The Eocene-Oligocene (*c.* 34 mya) boundary was marked by an unprecedented and abrupt cooling (Janis, 1993), much more pronounced than the gradual lowering of temperatures during the Eocene. This seems to have been caused by a combination of factors that included the opening of the Antarctic gateways and lowered atmospheric CO_2 levels, at a time when the Earth's orbit of the sun was at its most distant (therefore minimising solar insolation). Continental temperatures dropped by an average of 8.2°C in 400,000 years, and the first Antarctic ice sheets formed, but there was no corresponding increase in aridity (Zanazzi *et al.*, 2007).

After this, the continuing rise of the Tibetan massif, along with the elevation of the Rockies, Pyrenees, Carpathians, Zagros and other mountain ranges, during the Oligocene and into the Miocene contributed towards a global tendency towards aridity and the formation of the great deserts of today (Carrión, 2003). By restricting the flow of humid air beyond the mountain ranges, continental interiors dried up and more water was retained in the new polar ice caps.

Epoch	Fossil genera	Genera that became extinct	Genera extinction %
Eocene	77	54	70.13
Oligocene	44	15	34.09
Miocene	128	39	30.47
Pliocene	143	2	1.4
Pleistocene	187	0	0

Table 1.1 *Tertiary and Quaternary European fossil bird genera, and inter-epoch rates of extinction.*

The vegetation belts across Oligocene Holarctica were very different from those of the Eocene. The polar broadleaved forest disappeared and the belt of subtropical broadleaved evergreen woodland, which had occupied a high-latitude position, was displaced further south across much of the area taken up today by the Sahara, Arabia and across southern Asia to China. Instead the most northerly latitudes were taken over by a broad belt of temperate mixed (coniferous and deciduous) woodland, and to the south, across present-day temperate Eurasia and Northwest Africa, was a belt of temperate broadleaved deciduous woodland. Woody savannas were localised on the growing Tibetan Plateau. Tropical forest was limited to equatorial areas, with belts of seasonal paratropical forests to the north and south (Janis, 1993).

These changes are dramatically reflected in the number of avian genera that were lost between the Eocene and Oligocene. Following Mlíkovský's (2002) list of Cenozoic bird genera in Europe, I have calculated that more than 70% of the Eocene genera were extinct by the Oligocene, while just under 35% disappeared between the Oligocene and the Miocene (Table 1.1). Twenty-one new genera made their appearance in the Oligocene. There are no Palaeocene, and only two Late Eocene, genera represented among the Palearctic birds of today (Table 1.2). These are the *Recurvirostra* avocets and *Coturnix* quails. The number

Sub-epoch	Genera making first appearance	Genera still present today	Genera present today %
Late Palaeocene	2	0	0
Early Eocene	19	0	0
Mid-Eocene	20	0	0
Late Eocene	38	2	5.26
Early Oligocene	4	0	0
Mid-Oligocene	10	1	10
Late Oligocene	7	2	28.57
Early Miocene	46	20	43.48
Mid-Miocene	26	21	80.77
Late Miocene	27	21	77.78
Early Pliocene	16	14	87.5
Late Pliocene	38	38	100
Early Pleistocene	41	41	100
Mid-Pleistocene	2	2	100
Late Pleistocene	3	3	100
Holocene	2	2	100

Table 1.2 *Genera of European birds by first appearance and representation today.*

of Oligocene genera remaining in the present – *Puffinus* shearwaters, *Phoenicopterus* flamingoes and *Alcedo* kingfishers – is proportionately higher, though few in number. The Eocene–Oligocene transition reflects a major turnover of bird genera, which appears concomitant with the significant climatic and ecological changes that took place around 34 mya.

THE MIOCENE (23–5.33 mya)

By the start of the Miocene the world had been transformed. The world's land masses were practically in the positions of today, and polar ice caps had formed and grown (albeit non-permanently). As a result sea-levels had dropped significantly. Ecosystems and faunas were radically altered, the broadleaved forests of the poles vanished, and tropical forests were restricted to low latitudes. Among the mammals, herbivores increased in diversity and abundance and the first apes appeared on the scene (Finlayson, 2009). But the Miocene commenced with a period of global warming that lasted from 23 to 15 mya, during which time tropical and subtropical forests expanded once more within Africa and into Eurasia as far as Siberia and Kamchatka (Janis, 1993). A huge territory, from the Iberian Peninsula to China and from Kenya to Namibia, was a mass of tropical and subtropical forest across which a diversity of apes thrived (Begun, 2003), giving a clear indication of the climatic and ecological conditions across this huge area given the tropical requirements of apes today, confined as they are (bar humans, of course) to forested regions of Africa and South-east Asia.

Around 19 mya Africa and Arabia collided into Eurasia, severing the ancient Tethys Ocean and creating the Mediterranean Sea. The connection between Eurasia and Africa was intermittent until 14 mya. After that, and right up to today, Africa and Eurasia have formed a single land mass (Finlayson, 2009). The interlude of global warming at the start of the Miocene came to an end and the general downward trend in global temperatures was renewed around this time. Coincidental was a period of intense uplift of the Tibetan Plateau from 13 mya (Clark *et al.*, 2005), which may have continued regionally until after 7 mya (Wang *et al.,* 2006), the permanent establishment of the Antarctic ice cap, and the start of glacial climates in the Arctic (Carrión, 2003). Once more the tropical forests retreated and the northern hemisphere latitude vegetation belts restored, with notable innovations. The north was dominated once more by temperate woodland (of mixed coniferous and deciduous trees) with a wide band of temperate broadleaved deciduous woodland to its south. These forests resembled the modern taiga in character. The pattern resembled that of the end of the Oligocene, except the temperate broadleaved deciduous woodland did not extend south to the new Mediterranean Sea. There the vegetation across both shores of the sea, and south to the tropical zones, had a distinctly seasonal character, with winter rainfall and a summer dry season. The vegetation was dominated by forests of pines and oaks*,* with other typical components including cedars*,* hemlocks and *Arbutus* strawberry trees (Carrión, 2003).

To the east of the Mediterranean the paratropical forest, with summer rainfall, occupied a low latitude band across Arabia to China. This was dominated by beeches, laurels, pines and spruces*.* To its north was a band of subtropical woodland and woodland savanna, which included mangroves and swamps. This woodland included cypresses*,* maples, poplars*,* willows and oaks. South of the Mediterranean and paratropical belts lay the tropical forest, in Africa and across southern Asia (Janis, 1993). But the lifting of the Tibetan Plateau interrupted the mid-latitude belts, which were no longer continuous from east to west. Grasslands and steppe appeared for the first time, covering a large area of the arid continental interior of the Eastern and Central Palearctic. The wooded steppes were open and dominated by junipers and *Celtis* nettle trees. Temperate woodland, similar to that in the far north, appeared around the great mountain mass as it was elevated.

Grasses

A major and significant ecological novelty arose during the Miocene, one that would have a major impact on the world and from which many bird species would benefit. This was the emergence of the C4 grasses.

a

b

c

Figure 1.3 *Idealised representation of (a) Eocene and (b) Miocene bioclimates of the Old World compared to the present day (c). The Old World goes from domination by warm and wet tropical climates to the temperate and dry climates of today, with humid climates restricted to the tropics and oceanic seaboards. Key: 1 warm/wet (annual temperature T > 20°C, annual rainfall R > 1200mm); 2 warm/humid (T > 20°C, R 600-1200mm); 3 temperate/wet-humid (T 10–20°C, R > 600mm); 4 cool/ wet-humid (T 0–10°C; R > 600mm); 5 warm/dry (T > 20°C; R < 600mm); 6 temperate/dry (T 10–20°C; R < 600mm); 7 cold/dry (T < 0°C; R < 600mm). Based on sources cited in the text.*

19

Lineage	Eocene	Oligocene	Miocene	Pliocene	Pleistocene
1(a) (i) Shrikes, corvids, orioles			(1)/2	4	
1(a) (ii) Hirundines, warblers, larks			6	3	6
1 (a) (iii) Tits				2	
1 (a) (iv) Chats and thrushes			2	8	4
1 (a) (v) Sparrows, finches, buntings & pipits			4	7	4
1 (c) Falcons			1		
1 (d) Terrestrial non-passerines	(17)	(3)/1	(9)/3	1	2
1 (e) Owls	(6)	(1)	(4)/3	5	
1 (f) Diurnal Raptors	(1)	(2)	6	(1)/1	6
2 Shorebirds, gulls, terns and auks	1	(4)	(1)/7	6	11
3 Water birds	(10)	(3)/1	(9)/10	1	4
4 Cranes, rails, bustards and cuckoos	(12)	(1)	(7)/4	(1)/5	1
5 Swifts and nightjars	(12)		2		2
6 Pigeons, flamingoes and grebes	(2)	(1)/1	(2)/1	4	3
7 (a) Gamebirds	(5)/1		(2)/1	4	3
7 (b) Wildfowl	(5)	(3)	(3)/8	2	5
8 Ratites	(2)		1		

Table 1.3 *First presence of genera by epochs. Figures in table are number of genera. Numbers in brackets are extinct genera.*

Grasses were able to use a photosynthetic pathway different to that of established (C3) plants, and they did so most efficiently in warm climates with low CO_2 concentrations. They first appeared around 20–25 mya but had relatively little impact (Pagani *et al.*, 2005) until 6–8 mya, when decreases in atmospheric CO_2, coupled with enhanced aridity, gave these plants the edge in warm environments and they started to expand geographically (Cerling *et al.*, 1997; Pagani *et al.*,1999). This represented the start of the new world of grasslands and savannas. The expansion started in Africa around 8 mya in the equator and reached the cooler south of Africa by 5 mya (Ségalen *et al.*, 2007), but the process of expansion was protracted and there were important gains at 1.8 and 1 mya, by which time grassland had come to dominate large areas of tropical Africa.

The Miocene was a time of upheaval during which we detect the clearest signals of the modern avifauna of the Palearctic. We have seen that there was considerable loss of Oligocene bird genera, though not as spectacular as during the Eocene-Oligocene transition, and more disappeared during the Miocene, which represents the last epoch with major generic extinction (Table 1.3). The analysis presented in Table 1.3 is based on genera present in the European fossil record. It shows the Miocene as a key period in which loss of genera is compensated by a greater number of genera that persisted to the present day. Before the Miocene, extinction greatly exceeded persistence, and after this the pattern was reversed. The modern genera of Palearctic birds are therefore the product of accumulation since the Miocene.

When did migration commence?

To try to answer this important question I show in Table 1.4 the European fossil genera by epoch, and I have indicated those genera which today include migratory and trans-Saharan migratory species. This is an underestimate because we do not know how many other, extinct, genera might have also been migratory, and

Epoch	Genera Present	Migratory Genera	Trans-Saharan Genera
Eocene	76	2 (2.63%)	1 (1.32%)
Oligocene	43	4 (9.3%)	1 (1.32%)
Miocene	105	44 (41.91%)	22 (51.16%)
Pliocene	120	68 (56.67%)	37 (30.83%)
Pleistocene	164	106 (64.63%)	57 (34.76%)

Table 1.4 *Distribution of fossil migrant genera by epochs. Migratory genera refer to genera that today have migratory species.*

it is an approximation because it does not follow that these genera were migratory in the past. But, at least, we do know that they had the *potential* to become migratory. The results show a clear increase of migratory potential in the Miocene. The increase is not only absolute but is also proportional – there are more migratory genera that first appeared in the Miocene per total genera in the Miocene than before or after. There is also a sustained first appearance of more migratory genera after the Miocene suggesting a progressive build-up of migrants. If these results are correct then we can suggest that migratory behaviour in the Palearctic intensified during the Miocene and continued thereafter. Given what we have seen regarding the increased seasonality and reduction in tropical habitats from the mid-Miocene, this is not altogether surprising.

THE PLIOCENE (5.33–2.6 mya)

The Pliocene had an important prelude at the end of the Miocene. It was a protracted geological event with ecological implications as great as the uplift of the Tibetan Plateau. It commenced around 8.5 mya, well within the Miocene, with the restriction of water circulation from the Atlantic into the Mediterranean, as Africa closed into Europe. By then the eastern end of the Mediterranean Sea had closed as the Arabian Peninsula connected with the Eurasian landmass. Unlike today, Atlantic water entered the Mediterranean along two channels, but these became increasingly constrained as new land was uplifted by the pressure of the African plate as it pushed northwards. As insufficient water replenished evaporation, the Mediterranean started to become a series of saline lakes (Finlayson, 2009).

At 5.59 mya, the connection between the Mediterranean and the Atlantic was severed. This was a world of extreme aridity. But not all was dry and saline. One consequence of the desiccation of the Mediterranean was that a summer low pressure system developed over the hot and dry basin. With the south-westerly monsoons not fully fledged as Tibet continued to rise, the Mediterranean summer lows drew in moist air from the Indian Ocean, creating a south-easterly monsoon. Today's south-westerly monsoon draws moist air up to the Himalayas. The water is then discharged as rainfall, which feeds the major rivers that empty into the Bay of Bengal. But the south-easterly monsoons of the Miocene-Pliocene took this moist air towards north-east Africa and much of the eastern half of the present-day Sahara. We can see the remnants of this climatic period in Lake Chad and the Nile – this is what is left of what became a land of mega lakes. At its height, water collected in four huge basins within the Sahara. These became massive inland freshwater seas that drained northwards into the eastern Mediterranean. There the water dropped from great heights down massive cataracts into a saline lake (Lake Cyrenaica). The four lakes drained an area of 6.2 million square kilometres, an area eleven times the size of France (Griffin, 2002; Finlayson, 2009).

We get an inkling of what the environment around 'Lake Mega-Chad' was like in the Late Miocene and Pliocene from palaeontological work carried out in the area, which has produced some of the earliest known hominid fossils (*Sahelanthropus tchadensis*). These riverine and lake environments covered huge areas. Seasonally inundated lands and gallery forest interfaced directly with savanna and desert, generating a high diversity of life including freshwater fish, soft-shelled turtles, tortoises, pythons and lizards, mammals from

hippos to sabre-toothed cats to hyaenas, and a diverse community of water birds including cormorants, darters, ducks, storks and herons (Vignaud *et al.*, 2002; Louchart *et al.*, 2004). At this stage at least trans-Saharan migration would not have presented the kinds of problems that it would for birds in later times.

Filling the Mediterranean

The Miocene prelude was brought to a dramatic conclusion at the very start of the Pliocene, 5.33 mya. A river had been eroding land in the west of the Mediterranean Basin, cutting back slowly towards the Atlantic Ocean. When it reached the level of the Atlantic, which was 3000 metres above the dry basin to its east, oceanic water started trickling in. It was a slow trickle for a few decades (dated with extraordinary precision to 26 years; see Loget *et al.*, 2005 and Blanc, 2006), during which time it began to cut a deep channel. But once it opened up sufficiently a huge cataract of water fell down the abyss. The western basin of the Mediterranean filled within ten years, and water spilled over to the eastern basin, filling it in a year (Blanc, 2002; Loget and van den Driessche, 2006). The new sea altered the climate of Europe and North Africa almost overnight. The increasing trend towards the south-westerly monsoon, as Tibet's influence magnified and the Mediterranean summer low disappeared, generated aridity, and modern types of desert, semi-desert and arid grasslands began to spread. The world's climatic and vegetation zones were beginning to increasingly resemble those of today. The warm, wet and forested planet was gone. Rainforests were shrinking in extent and woodlands had started to break up; this was a significant time in the evolution of the early human lineage (Finlayson, 2009).

In parallel with these events, Central Asia started to become increasingly arid in the Early Miocene (*c.* 22 mya). The trend towards a windier and drier climate intensified in the Late Miocene (there were peaks of dust accumulation at 13–15 and 7–8 mya) and especially in the Pliocene and Pleistocene, after 3.5 mya (Guo *et al.*, 2002). These events were related to the periodic expansion of sea ice in the Arctic Ocean and the appearance of ice sheets in northern Eurasia. We should recall here that the separation of azure-winged magpie populations coincided with the Pliocene intensification of Central Asian aridity, and this phenomenon has been implicated in the isolation of other birds across Eurasia, with consequent speciation that can be linked to periods of aridity when deserts isolated populations of forest and other birds (Voelker, 2010). Significant changes seem to have affected Palearctic mammals during this time, too, with a notable increase in hypsodont species (with high-crowned teeth and enamel allowing for greater wear) and grazers, reflecting the shift towards more open biomes (Fortelius *et al.,* 2006).

Birds of arid and montane habitats

Given this ecological scenario it is not surprising to find bird genera typical of arid habitats as well as those of rocky and montane habitats appearing for the first time in the Pliocene fossil record – the *Tetrax* bustards, *Charadrius* plovers, *Gyps* vultures, *Athene* owls, *Streptopelia* doves, *Falco* falcons, *Alauda* and *Eremophila* larks, *Pyrrhocorax* choughs, *Oenanthe* wheatears, *Monticola* rock thrushes, *Prunella* accentors and *Emberiza* buntings. The rate of genera extinction between Miocene and Pliocene was comparable to that between Oligocene and Miocene, not surprising perhaps given the ecological changes described above, but it was on a scale lower than at the Eocene-Oligocene transition (Table 1.1). If we attempt to provide an estimate of new genera per sub-epoch, taking the length of each into account, we find that there have been three peaks of genera formation: (a) Late Eocene; (b) Early Miocene; and (c) Early Pliocene-Early Pleistocene. We have to treat these results with some caution as there is likely to be a bias towards the present (since more recent fossils stand a better chance of preservation), and the first fossil dates need not represent first appearance. The Pliocene to Early Pleistocene stands out as a point at which many new genera make their first appearance. The Early Miocene is its prelude. In contrast, the Middle-Late Pleistocene seems insignificant in comparison.

CHAPTER 2

The changing ecology of the Palearctic in the Pleistocene

I showed in the previous chapter that the Pleistocene was relatively insignificant in terms of species formation and extinction, and that it was range shifts, contractions and expansions that instead characterised this period. The reasons for the difference with the preceding Miocene and Pliocene, when range shifts presumably also played some part, are the shortness of this period and the increasing small-scale climatic oscillations in the coldest and driest world since the K/T Event. I attribute the poverty of new species and genera to lack of time and directional climatic trends. The absence of significant extinction is, in my view, attributable to the fact that weeding had occurred in the Miocene and to a lesser degree Pliocene, so that the species that reached the start of the Pleistocene, and ultimately made it to today, were the survivors.

This message is reinforced in Figure 2.1, which shows the first recorded presence of present-day species in the European fossil record (Mlíkovský, 2002). The picture is clear: most species appear during the Pliocene and Early Pleistocene and very few do so after this (after *c.* 780,000 years ago). Bearing in mind first fossil records probably mean that the species were present before that, and seeing the clear peak in species during the Late Pliocene and Early Pleistocene, we can conclude that the emergence of modern Palearctic species (in most cases evolving from ancestral species present since the Miocene) happened around 3.5 mya and after that. This date coincides with the main period of Central Asian desert formation, and comes after the opening of the Strait of Gibraltar and the flooding of the Mediterranean Sea, with the consequent
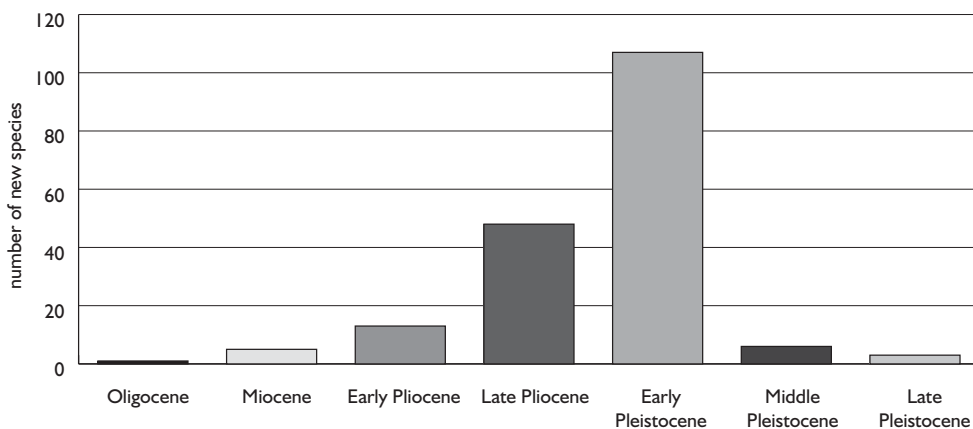
Figure 2.1 *First presence of Palearctic bird species in the fossil record. The importance of the Late Pliocene and Early Pleistocene in generating novelty at species level is clear, and contrasts with the comparative insignificance of the Middle and Late Pleistocene. Early Pliocene (5.33–3.6 mya), Late Pliocene (3.6–1.8 mya), Early Pleistocene (1.8–0.78 mya), Middle Pleistocene (0.78– 0.125 mya), Late Pleistocene (0.125–0.01 mya). Note the boundary of the Pliocene-Pleistocene has recently been revised to 2.588 mya but I have kept to the earlier boundary as fossil sites employed in this analysis have used the earlier definition. For the purposes of this analysis, the importance of the Late Pliocene–Early Pleistocene is not affected.*

aridification of the climate of the Palearctic. The emergence of modern species therefore has much more to do with habitat fragmentation caused by aridity than with the waves of cold that engulfed the Palearctic, especially from the Middle Pleistocene. This result is supported by Voelker's (2010) genetic study of a range of Palearctic songbirds that became isolated and split into different species precisely at this time, and as a result of the expansion of the deserts of Central Asia.

THE CLIMATE OF THE PLEISTOCENE

During the Pleistocene, the world came under the increasing grip of cold periods (or glacials), usually though not always accompanied by aridity, and climatic instability. The harsh conditions intensified at the start of the Middle Pleistocene (*c.* 780,000 years ago), when the Earth's climate came under the grip of 100,000-year cycles of cold and warm (caused by regular and periodic changes in the Earth's orbit, tilt and wobble), which replaced the lower amplitude climatic oscillations (in 41,000-year cycles) of the Early Pleistocene (Ruddiman *et al.*, 1986). The world of the Middle Pleistocene was a colder one than that which preceded it in the Late Pliocene and Early Pleistocene, especially after 400,000 years ago. The glacials were preceded and succeeded by long periods when temperatures were returning from or heading towards warm maxima; these interglacials, which at times saw temperatures higher than those of today, were short, lasted around 10,000 years (Burroughs, 2005) and took up no more than 10% of the Pleistocene (Lambeck *et al.*, 2002 a, b). For much of the Pleistocene the Palearctic was a colder place than it is today.

Climatic variations

At millennial scales the dominant climate cycles are known as Dansgaard-Oeschger (DO) temperature oscillations. These were linked with the alternation between warm periods and glacials and stadials (shorter episodes of ice expansion during warm interglacials) in the North Atlantic (Dansgaard *et al.*, 1993; Alley *et al.*, 1999). Less frequent, and of shorter duration, were moments of intense cold which were the result of massive discharges of ice as the Laurentide Ice sheet surged through the Hudson Strait. These events are known as Heinrich Events (Heinrich, 1988; Bond and Lotti, 1995: Alley *et al.*, 1999). There were also brief periods of warming in the midst of glacials (interstadials), all of which added to the general climatic instability (A. Voelker, 2002). Typical of lower latitudes were alternating phases of rainfall (pluvials) and aridity (inter-pluvials) which would have had a particular bearing on Palearctic birds that migrated to these latitudes in the winter. These oscillations caused repeated advances and contractions of forest and open habitats in Europe and semi-desert in the Mediterranean and North Africa.

A characteristic feature of these cycles of cold and warm, wet and dry, was the speed of change. Global warming at the start of the last interglacial was estimated at 5.2°C per thousand years (Ruddiman and McIntyre, 1977) and temperatures rose by 7°C in 50 years at the end of the last glacial maximum (LGM) (Dansgaard *et al.*, 1989) while Stuiver and Grootes (2000) recorded 13 cold-warm transitions between 60,000 and 10,000 years ago, each of which took 50 years to complete. An early study revealed that the temperate forests of northern France were replaced by pine, spruce and birch taiga at the end of the last interglacial in the space of between 75 and 225 years (Woillard, 1979), and in Italy changes in vegetation were rapid over the last 102,000 years, with forest and wooded steppe biomes replacing steppe and back, at an average interval of 142 years (Allen *et al.*, 1999). These rapid changes in vegetation would ultimately have affected many terrestrial vertebrates, including birds, in the Palearctic (Finlayson and Carrión, 2007).

Mammals responded to the onset of the 100,000-year cycles at the start of the Middle Pleistocene by contracting or shifting geographical range, by immigration from northerly latitudes and by adaptation to the new conditions. There was extinction too, all of which contributed to a drastic reorganisation of the Palearctic mammalian fauna (Finlayson, 2009). In contrast, as we have seen, there was relatively little speciation or extinction among the Palearctic's birds, which instead seem to have responded by adjusting their geographical ranges. Specific examples will be discussed in the species accounts in the following chapters.
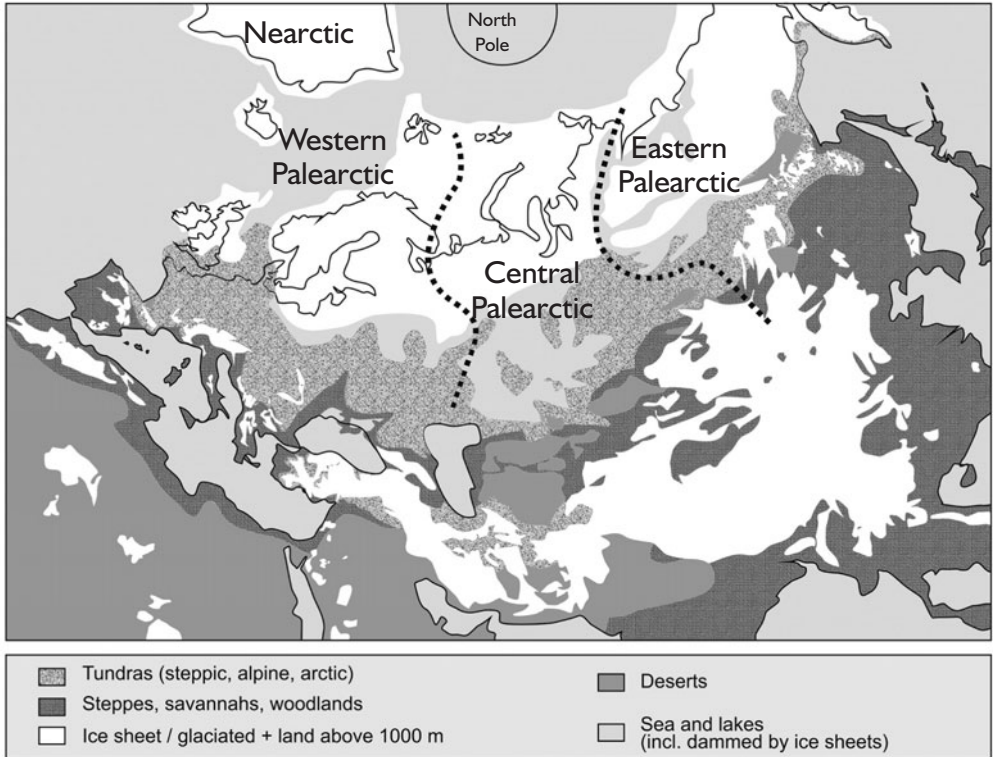
Figure 2.2 *The Palearctic at the last glacial maximum. Note the huge areas covered by ice, ice-dammed lakes, and tundra, all of which would have had a significant impact on the distribution of Palearctic breeding birds. This map shows the boundaries of the Western, Central and Eastern Palearctic adopted throughout this book. Map courtesy of Professor J. S. Carrión, University of Murcia.*

Sea levels

During the cold glacials, sea-level dropped between 90 and 130m below present levels (Shackleton and Opdyke, 1976; Rohling *et al.*, 1998, Lambeck *et al.*, 2002a), creating large expanses of coastal habitat in many areas that are now submerged. Sea-level high-stands (sometimes higher than present levels) were associated with interglacials. In general, sea-level rise appears to have been rapid. During the deglaciation leading to the last interglacial (known to geologists as the Marine Isotope Stage (or MIS) 6), sea-level rise was of the order of 20m per 1,000 years, and sea-levels reached between 2 and 12m above the present level (van Andel and Tzedakis, 1996). The subsequent drop towards the LGM was of the order of between -118 and -135m below present levels (Clark and Mix, 2002).

The barriers that were formed by the glaciations, and the land bridges that reopened as sea levels dropped with the cold, did cause isolation and reorganisation of geographical ranges, as the Central Asian desert formation had done previously. There seems to have been some level of lineage-splitting among some birds (Voelker, 2010) but at a smaller scale than in the Pliocene. It seems likely that the rapid shifts in climate did not allow sufficient time for much more, and what we do observe is part of a protracted process of lineage differentiation which, in the Pleistocene, occurred largely at the level of populations, subspecies or very closely related species. This differentiation seems to have taken place largely in refugia (places where animals and plants survived during the worst moments of the glaciations), particularly in the Iberian Peninsula, Italy, the Balkans, the Caucasus, and parts of southern Siberia. This has been amply documented for a variety of animals and plants, and it is in such refugia that a wide range of species, including humans, survived

(Hewitt, 1996, 2000; Willis, 1996; Taberlet *et al.,* 1998; Willis *et al.*, 2000; Taberlet and Cheddadi, 2002; Finlayson *et al.*, 2006). There is also increasing evidence that some species survived further north in what have been termed 'cryptic' refugia (Stewart and Lister, 2001), all of which adds up to a picture of survival of the most adaptable species in a range of geographical locations, from which they re-colonised other parts of the Palearctic when climatic conditions improved.

The last glacial cycle

The toughest period climatically of all was that from 125,000 to 10,000 years ago, the last glacial cycle, which covered the Late Pleistocene. Some of the remaining warm-climate mammals from the Palearctic (Straight-tusked Elephant *Elephas antiquus*, Narrow-nosed Rhinoceros *Stephanorhinus hemitoechus*, Barbary Macaque *Macaca sylvanus*, Hippopotamus *Hippopotamus amphibius*, European Water Buffalo *Bubalus murrensis*) did not make it and were gone early in this period, which came to be dominated by cold steppe-tundra mammals (Woolly Mammoth *Mammuthus primigenius*, Woolly Rhinoceros *Coelodonta antiquitatis*, Reindeer *Rangifer tarandus*, Musk Ox *Ovibos moschatus*, Irish Elk *Megaloceros giganteus,* Arctic Fox *Alopex lagopus*) of the Palearctic, with periodic westward range extensions of arid Central Asian mammals (particularly Saiga Antelope *Saiga tatarica*) as far as the Iberian Peninsula.

The severity of the last glacial cycle illustrates the radical changes that the birds of the Palearctic were subjected to. It was the culmination of the progressive climatic deterioration and increasing instability that marked the Pleistocene as a result of the progressive glaciation of the northern hemisphere (Finlayson, 2004). It marked the final contraction and extinction of all tropical and subtropical woodland from southern Europe, and the rise and geographical expansion of xeric (dry-adapted) plants during the LGM, around 20,000 years ago (Carrión *et al.*, 2000).

The last glacial cycle started with the significant warming and melting of ice around 130,000 years ago, which led to a brief interglacial (known as MIS 5e) when global temperatures were warmer than today. This was followed by a rapid climatic deterioration towards a glacial at 75,000 years ago (MIS 4), then a long period of ice withdrawal before the next, and most severe, advance towards the LGM (*c.* 20,000 years ago – MIS 2), when the Atlantic polar front reached a latitude of 38^{0}N (the position of Lisbon) at the LGM (Calvo *et al.*, 2001). Between the two glacials, between 60,000 and 25,000 years ago, temperatures were lower than in the interglacials but higher than during the glacials. This was a long period, covering 35,000 years, which was typified by the high variability of the climate at the scale of millennia, centuries and even decades (van Andel and Tzedakis, 1996). Intense cold, aridity and climatic instability were the hallmark of the last glacial cycle that the Earth has experienced to date.

CHANGES IN REGIONAL ECOLOGY

The Eurasian Plain

This is the vast region of lowlands that spans the Palearctic, from the British Isles to the Pacific east. The way in which trees colonised this vast area during interglacials was heavily dependent on where they started from (*i.e.* the location of the glacial refugia) and the speed and duration of warm conditions. Some interglacials were more humid (or oceanic) than others, and this also added to the variability of the vegetation's response (Zagwijn, 1992). Much of Europe was covered by temperate mixed oak forest during the last interglacial (Vandenberghe *et al.*, 1998; Turner, 2002; Kukla *et al.,* 2002). This was an oceanic interglacial, a relatively uncommon type that only took up 12% of the whole of the last 500,000 years, and typified by a continuous sequence of geographical expansion of elm *Ulmus,* oak *Quercus,* hazel *Corylus,* yew *Taxus,* and hornbeam *Carpinus*, and then by fir *Abies,* spruce *Picea* and pine *Pinus.* The response of trees to warming during the continental interglacials was significantly slower.

At the other end of the scale, at the height of the LGM, two-thirds of the British Isles was under glaciers, as was much of Scandinavia, the Baltic and the Alps. The rest of Europe north of the Mediterranean region was under permafrost (CLIMAP, 1976; Maarveld, 1976). In ice-free areas bare ground and a strange flora predominated, usually low in height and poor in cover (Birks, 1986; Zagwijn, 1992; Finlayson and Carrión, 2007). In general, the Eurasian plain during this glaciation was desolate, with tundra, pockets of sparse vegetation and scattered and isolated refugia of trees (Figure 2.2). The severity of the climate was made worse by abruptness of the changes (Allen *et al.*, 1999; Barron *et al.*, 2004; Tzedakis, 2005). This severity is reflected by temperature estimates based on the presence of beetles that are sensitive to such changes (Coope, 2002); during the build-up to the LGM, between 40,000 and 25,000 years ago, the mean July temperature in the British Isles (an oceanic temperate region) was close to 10°C and winter temperatures were around -20°C. Summer temperatures were close to the lower limit below which tree growth could not take place.

In summary, it seems that the vegetation of the Eurasian plain, in the west at least, oscillated between conifer woodland, with shrub tundra to the north, when it was warm, and a tundra-cold steppe mosaic with polar deserts to the north during the coldest periods (van Andel and Tzedakis, 1996; Finlayson and Carrión, 2007).

To the east, on the Russian plain, an open and harsh steppe replaced the dense temperate forests of the interglacials (Rousseau *et al.,* 2001) as the climate became increasingly arid and continental prior to the LGM (Soffer, 1985). Large tracts of land suffered extremely low temperatures, high aridity and a covering of permafrost. The cold steppe was a unique combination of tundra, steppe and grassland, punctuated by sparse arboreal vegetation, even during the coldest periods, of pine, beech and oak along the rivers valleys. These may have provided refugia for some species of birds.

During a brief respite, around 33,000–24,000 years ago (known as the Briansk Interstadial), a mix of tundra, forest-tundra and tundra-steppe covered the Russian plain. The southern limit of Arctic plants was nonetheless 1200 km further south than it is today, and it reached a further 600 km further south during the LGM. The southern Russian plain was milder, especially around the Black Sea, where steppe and forest-steppe predominated. The Crimean Peninsula, with its topographic variability that contrasted with the stark flatness to the north, allowed a greater diversity of vegetation to survive (Markova *et al.*, 2002). These temporary climatic improvements were also noticeable to the north. In northern Siberia, open larch forest with alder *Alnus glutinosa* and dwarf birch *Betula nana* developed in the Taimyr Peninsula between 48,000 and 25,000 years ago (Andreev *et al.*, 2002).

With the passing of the LGM there was a noticeable thermal improvement by 14,700 years ago, which lasted 2,000 years, and boreal woodland started to replace steppe and tundra in north-western Europe. Spruce forest and birch-conifer woodland followed (Huntley and Birks, 1983). This was the time when humans are thought to have entered North America. A brief reversal, known as the Younger Dryas, between 12,900 and 11,600 years ago (Burroughs, 2005) brought the tundra back as far south as France and the British Isles, but rapid climatic amelioration leading to the conditions of the present day followed after 11,000 years ago, and today's climatic world had taken shape by 10,000 years ago. Woodland took over as steppe retreated to Central Asia and tundra to the Arctic.

One dramatic aspect of the Last Glacial Cycle, of huge potential importance to populations of Palearctic waterbirds, was the emergence of gigantic inland freshwater seas across Siberia during this time (Figure 2.2). These were created as ice sheets covered the Russian Arctic, preventing the outflow of water from the Siberian rivers northwards. The corresponding wetland habitats that would have emerged on the margins must have attracted vast numbers of waterbirds and the present, fragmented, distribution of a number of these species (which we will see in the species accounts) may be a reflection of the loss of this former waterbird paradise. When the climate warmed the ice dams became unstable and large areas suffered cataclysmic superfloods (Rudoy, 2002; Finlayson and Carrión, 2007).

I end this section with a note of caution. For too long we have been given the image, partly reflected above, of a Eurasian plain that was either forested or denuded of vegetation. But we have seen already that glacials and interglacials only covered a small fraction of the time, most of which was taken up toing and

froing between the two extremes. This means that for large periods vegetation was also shifting between these extremes, creating regional mosaics of habitat, many of which were neither dense forest nor treeless plains. It seems that even during the warm interglacials patches of open vegetation persisted within forests, along floodplains, on areas with infertile soils, and in continental and sub-Mediterranean areas (Svenning, 2002). This observation has significant implications for the survival of Palearctic birds during glacial cycles, and has been hitherto unappreciated.

The mid-latitude belt

One major change that I have not yet commented on is the emergence of the mountain chains that resulted from the process of collision of Africa, Arabia and India into Eurasia. We have seen how the uplift of the Tibetan massif had profound implications for the climates, biomes and animals of the Palearctic. But the change that I am referring to here was the emergence of a belt of varied topography, contrasting with the flat expanses of the Eurasian plain to the north, which ran from the Himalayas west to the Iberian Peninsula. I have referred to this mid-latitude belt (MLB) earlier in this book (see p. 10). The important point to note now is that it created, from the Miocene onwards, a discontinuity in the arrangement of the vegetation belts that had previously followed a latitudinal pattern. On the Eurasian plain, arctic, boreal and temperate belts continued to respect latitude, but the MLB became a source of fragmentation and discontinuity that would have significant implications for speciation and geographical range in many species. In addition, the potent combination of high mountains, deserts (to which we can include the Sahara) and the Mediterranean Sea created an effective barrier that severed the connection between the Palearctic and the tropics, except in the Far East.

The best-studied part of the MLB is the west, where the Mediterranean and proximity to the Atlantic generated unusual oceanic conditions that contrasted with the much more arid conditions of the central and eastern MLB, where the highest mountains also happened to be located. The climatic conditions of the MLB would have varied in a similar manner to those of the Eurasian plain, except that the regions closest to the high mountains would have suffered severely from the local formation and expansion of mountain glaciers and the loss of water supply to the continental areas, which consequently became massive deserts. Geography and local climatic peculiarities controlled vegetation much more closely than on the Eurasian plain (Suc *et al.*, 1994).
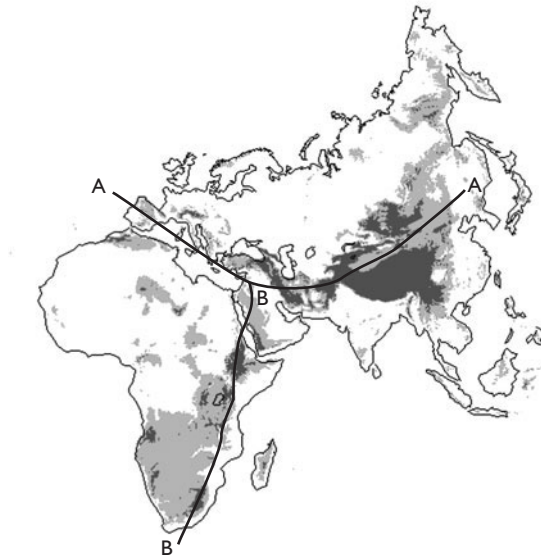

Figure 2.3. *The mid-latitude belt of heterogeneous topography. Land between 750m and 1500m in light grey; land over 1500m darker grey. Line A–A indicates the approximate mid-line of the belt. Line B–B indicates the southward extension to South Africa.*

The width of the Mediterranean and the major mountain masses of the MLB became barriers for plant and animal movement. One feature of the MLB was the extension of high ground well south, and this feature permitted the corresponding intrusion, and later survival, of temperate and boreal vegetation (Rivas-Martínez, 1981, 1987; Zagwijn, 1992). The effect was not limited to plants; we will discover a number of birds with geographical ranges that reflect these southward intrusions during glacials.

A major difference from the Eurasian plain across much of the MLB was the importance of moisture as a critical bioclimatic variable, with temperature playing a supporting role (Tzedakis, 1994; Willis, 1996). The influence of wet and dry cycles, which resembled those of tropical latitudes, would have varied at different points of the glacial cycles (Narcisi, 2001). Many areas of the MLB would have experienced harsh climatic conditions during glacials and stadials (Rose *et al.*, 1999) but there would have been areas of relative stability (Prokopenko *et al.*, 2002) and localised refugia which, even during the coldest periods, would have retained a warm and wet climate. The most notable of these were at the two extremes of the MLB, the south-western Iberian Peninsula and south-eastern China (Finlayson and Carrión, 2007). Significant patches of Mediterranean vegetation survived even the coldest and driest moments, and these areas provided major refugia for many bird species.

Shifts from forest cover to open vegetation in the MLB were even more abrupt, given the influence of altitude bands in close proximity to each other (Peteet, 2000), than on the Eurasian plain. Tzedakis (1994) reported that between 70 and 80% of each glacial-interglacial cycle was taken up by intermediate conditions between forest and treeless habitats. This observation recalls that made for the Eurasian plain, but in the MLB, with its topographic heterogeneity at small scales, the vegetation mosaics and patterns were more diverse and continuously changing.

In Greece, the intermediate periods were characterised by steppe-forest, forest-steppe and steppe vegetation, with the extremes being desert-steppe and forest (Tzedakis, 1994). In Italy open and arid habitats were also typical of glacials with less open, humid, environments during interglacials (Montuire and Marcolini, 2002). In Iberia, habitats ranged from open steppe in the central areas during the coldest moments through conifer steppe during cold and arid phases on the coast to Mediterranean woodland in the warmest times. In the south-western Iberian refugium conditions varied little from warm savannas and woodlands at any stage, with only the intrusion of montane pines in the coldest moments being indicative of change. These southerly latitudes never received the cold steppe-tundra mammal fauna, which did not stray much further south than the level of Madrid, but Arctic seabirds did reach the latitude of Gibraltar, suggesting increased summer-winter seasonality (Finlayson and Carrión, 2007).

One final note of interest concerns the differences between the various glacial refugia in terms of the nature of the vegetation that each harboured. The western Balkans, and to a lesser degree the Alps and the Italian mountains, seem to have been the major European refugia for broadleaved trees during the last glaciation (Bennett *et al.*, 1991; Zagwijn, 1992; Willis, 1996; Tzedakis *et al.*, 2002). The Iberian Peninsula was, instead, a refugium of sclerophyllous (dry scrub) Mediterranean vegetation (Carrión *et al.*, 2000; Finlayson, 2006). The Near East and south-western Asia were arid and not as important as refugia for temperate plants. In North Africa, the southward migration of the dry subtropical high-pressure zone during glacials generated aridity with a reduction of Mediterranean woodland at the expense of steppe and semi-desert (Hooghiemstra *et al.*, 1992; Dupont, 1993). These vegetational differences had implications for birds also reliant on these refugia.

The Sahara

The Sahara, the northern half of which marks the southern boundary of the Western Palearctic, is a major feature of direct and critical importance to Palearctic birds, especially those that perform long migrations over it. This boundary between the Palearctic and the Afrotropical zoogeographical regions has not always occupied this position (around 30°N) but has instead shifted significantly since the Miocene (starting 23 mya), reaching at times a northerly position at 50°N (Pickford and Morales, 1994). During these moments, the African influence on the Palearctic was high and is reflected, for example, in the presence of crocodiles

in the Iberian Peninsula at 23–22, 18–16, 9 and 7.5–5.0 mya. When in this position there was climatic continuity between west and east from Iberia to China, which facilitated faunal interchange. The last time this occurred was in the Pliocene, around 3 mya, a time that we have already identified as critical for Palearctic birds, with significant disruption of geographical ranges.

A major shift towards increased cooling and aridity of the African climate started at the end of the Pliocene, around 2.8 mya, and it marked the wet and dry oscillations that have characterised it since that time (deMenocal, 1995). In north-east Africa the climate became progressively drier for long periods that were interspersed by short pluvial episodes (Crombie *et al.*, 1997). During the Middle Pleistocene a notable increase of aridity occurred after 200,000 years ago (Jahns *et al.*, 1998).

The north-west African climate has been very variable over the past 100,000 years, with a succession of wet and dry phases lasting between 1,000 and 10,000 years. The Sahel was largely vegetated for much of the last glacial cycle; the dominant vegetation was grassland that showed sudden and sharp peaks of expansion and contraction, with major expansions around 105,000, 80,000 and 10,000 years ago in the Sahara itself, at times when trees became important in the Sahel (Tjallingii *et al.*, 2008). The most recent wet phase lasted from 10,000 to 5,000 years ago, once the Holocene global warming had started; at this time the Sahara was covered by tropical grasslands, with forests and large permanent lakes (deMenocal, 2008). This was the last time that 'Lake Mega-Chad', which had its origins in the south-easterly monsoonal regimes of the Late Miocene (see p. 21), extended over a huge area (more than 400,000 km^2 – larger than the Caspian Sea, and up to 173m deep) (Drake and Bristow, 2006; Schuster *et al.*, 2005; Sepulchre *et al.*, 2008).

The ecology of this vast area, comparable in size to the United States, was rich and beautifully represented in the rock art painted by people who lived in a lush environment where desert now reigns (Roberts, 1998). This also means that as recently as 5,000 years ago, Palearctic-African migratory birds had an easy passage across the Sahara, which must also have been a hugely important breeding area for many species of wetland and grassland birds. But the abrupt loss of this ecologically rich region to desert that followed was part of a series of millennial dry-wet oscillations that had affected this region since the Middle Pleistocene, and embedded in the deeper trend toward aridity that has affected this region of Africa since the end of the Pliocene.

Tropical wintering areas of Palearctic migrants

A description of the tropical areas of Africa and southern Asia is beyond the scope of this book, but comment is warranted before concluding this chapter. The cold-warm cycles that affected the northern hemisphere also were largely replaced by wet-dry oscillations in the mid-latitude belt and Sahara and were also the dominant force in the tropics (deMenocal, 1995); this was reflected in expansion and contraction of tropical rainforest and mangrove at the expense of savanna and grassland in Africa (Lezine *et al.*, 1995). These broad changes would have affected differentially the wintering areas of Palearctic migrants which would, overall, have benefitted during the driest phases when rainforest extent was reduced and savanna and grassland extent was greatest, given that few Palearctic migrants winter in tropical rainforest (Moreau, 1972). South-east Asia remained wetter than Africa but was not exempt from the effects of aridity. There, too, rainforest gave way to savanna at times that coincided with significant lowering of sea-levels, which exposed large areas of land (e.g. Sundaland, a vast area including the islands of modern Malaysia and Indonesia east to the Wallace Line) (Bird *et al.*, 2005). In between, Arabia and southern Asia resembled North Africa more than South-east Asia in the response of vegetation to climate change, with huge areas taken over by desert during dry phases, and dry forest and savanna occupying tropical areas of south Asia (Field and Lahr, 2005).

CHAPTER 3
Origins of Palearctic birds

The preceding chapters have set the climatic and ecological scene that led to the origins of the Palearctic avifauna. In the species chapters that follow we will see how these origins appear to have been *in situ* within the large area of tropical and subtropical bioclimates that constituted the Eurasian-African land mass, together with an element of immigration that was overwhelmingly from South-east Asia, with a smaller fraction from the Nearctic and a relatively tiny contribution from Africa. The Palearctic avifauna's lineages are ancient, in most cases dating back to the Cretaceous (and therefore predating the K/T event that led to the extinction of the dinosaurs). The climatic events of the Eocene and Oligocene seem to have weeded out many genera that were unsuited to the cooling and drying world that was developing, while others were becoming confined to the tropical forests that were being restricted to low latitudes. Many of these genera still persist in the tropics of America, Africa and southern Asia and are effectively imprisoned within these warm and wet, mainly forested, environments.

Groups that remained within the Palearctic entered a phase in which new body plans, suited to a world of cool and dry bioclimates, emerged during the Miocene, a point that saw the end of the last lineages that had done well in the warm world of the early Tertiary and the beginning of a radiation of new forms that were able to handle the new ecological conditions. The culprit of this ecological change seems to have been the uplift of the Tibetan plateau, assisted by the re-organisation of ocean circulation resulting from the rearrangement of the continents. Ultimately, the extant Palearctic avifauna is the product of plate tectonics.

In the overall picture of climate change and the origins of new genera and species of Palearctic birds, aridity seems to have played a greater role than temperature. Aridity in northern Africa and Arabia replaced a land of mega-lakes at the start of the Pliocene. Wet and dry oscillations became typical of the African climate after 2.8 mya, and the Sahara experienced repeated phases of wet and dry that continued to the present day, the last wet period having ended as recently as 5,000 years ago. Similarly, the Central Asian deserts had been forming since the Miocene. By the end of the Pliocene a wide band of desert and semi-desert, stretching from north-west Africa, across the Sahara and Arabia and across Central Asia, dominated the middle and lower latitudes of the Palearctic.

Added to this new phenomenon were the expansion of the grasses and the emergence of grasslands and savannas across this belt. A huge area, once the domain of tropical forests, was now taken over by largely treeless habitats that fluctuated, depending on climate, between savannas, grasslands and wetlands on the one hand and deserts and semi-deserts on the other. A new habitat of huge extent, and a constant in this changing world had also arrived. This was the world of rocky habitats that provided a continuous habitat chain from the Himalayas to the Atlantic margin of the Palearctic.

So this was the new world the Palearctic avifauna faced at the start of the Pleistocene. These groups had run the gauntlet of climate deterioration and seemed built to last. They were the survivors. So when the glaciations hit the Palearctic, these birds had enough in them to allow them to survive everything that was thrown at them. The climatic changes of the Pleistocene were too many, too short and too fast to allow novelty and, instead, birds moved around the continental land mass, some faring better than others, as ecological conditions changed. Those that did well in wetlands received the bonus of the formation of large inland freshwater seas in Siberia.

The species accounts

Having introduced the story of the climate and the birds of the Palearctic, it is now time to take a closer look at the species. The data on which the analyses are based are presented in Appendix 1 (see p. 242), which includes 862 species, 556 of which breed in the Western Palearctic. This book concentrates solely on species that breed in the Palearctic. I do not include vagrants or migratory species that pass through the region but do not breed there. My analysis of information is based exclusively on climatic conditions, habitat and ecology in the breeding areas.

When I plan a long trip in the car, I take out a map with a scale that allows me to plan the entire route. These maps summarise the route and sacrifice a great deal of detail that would get in my way. The essentials are there, the main roads, main towns and distances that will allow me to get to the desired location. Once there a more detailed map allows me to navigate streets and roads to find my final destination. That detailed map would have been useless at the start of the journey as too much detail would have prevented me from understanding the route. In the same way, my aim here is to provide a road map, which is the history of the birds of the Palearctic, from which we can then look at species in greater detail. But we cannot begin to understand the detail without the big picture. This is why I never fully understood my swifts (see p. 8) – I was looking at them from too close. But that proximity makes sense now that I understand their bigger picture. Like the road map, to be able to make sense of the mass of data that emerge from looking at so many species, I have had to simplify the information. So I look at forests as a structural habitat in which trees occur at high density but I dispense with distinguishing between types of forest, not because these details are not important but because it would provide unnecessary clutter and prevent us from getting to our destination.

The dataset has the following headings:

(a) Bioclimatic tolerance

Each species is given a rank based on an examination of the breeding distribution of each species globally and compared with a bioclimatic map of the world (see Figure 1.3c, p. 19). Tolerance is a measure of how many of the bioclimates on the map the species occupies:

> A = specialist (occupies between 1 and 20%)
> B = semi-specialist (21–40%)
> C = moderate (41-60%)
> D = semi-generalist (61–80%);
> E = generalist (81–100%)

Bioclimatic tolerance is a reflection of a species' ability to live in a wide range of ecological contexts in a range of climates. It is not a measure of ability to withstand extremes of climate, but rather to survive in a range of climate-modulated environments, hence bioclimates.

(b) Latitude

Each species is allocated a latitude band on which its geographical range is centred.

> A = arctic (70°N)
> B = boreal (60°N)
> C = temperate (50°N)
> D = mid-latitude belt (warm species) (40°N)
> E = subtropical (30°N)
> F= multilatitude – species occupies several latitude bands.

(c) Temperature

From the global maps used to calculate tolerance, each species is given a position on a temperature gradient that goes from cold (1%) to hot (100%). Species at the cold end (between 1% and 20%) are A; this is followed by B (21–40%), C (41–60%), D (61–80%) and the warmest, E (81–100%).