Preface

Birds are feathered quadruped vertebrates who use their front legs as wings. The number of recognized species approaches 10,000. Not all birds fly. There are about 8500 extant volant species and each one flies in its own particular way. The variation is tremendous although birds also share common characteristics directly related to flight. Both the diversity and the basic requirements are fascinating. The fact that vertebrate structure and movement, adapted to satisfy aerodynamic principles, can defeat gravity is fascinating and we want to know how it is achieved. A variety of disciplines is involved in the subject. The demands of the physical laws governing the conquest of the air are clearly reflected in details of morphological, physiological and behavioural adaptations. A large body of knowledge is dispersed in specialized literature and is not easily accessible. Aerodynamic principles are often described in mathematical terms in papers where there is no room for explanations aimed at those primarily interested in birds. On the other hand, the complexity of the biological phenomena is difficult to grasp for scholars who are physically and mathematically orientated. I would like to display the interrelationships among the variety of aspects around avian flight in an attempt to make the subject comprehensible for interested readers from all disciplines.

Structure and function of bird wings differ fundamentally from aircraft wings in many ways. Bird wings consist of an arm and a hand part and can be stretched and folded. During gliding and flapping flight the wing shape can change dramatically. Flapping wings provide both lift and thrust and not just lift forces. It will become clear that aerodynamic theories explaining how conventional aeroplanes fly, are not sufficient to clarify flapping and gliding flight in birds. Most birds can land on a branch. To understand how they do that is an objective of this book.

'Avian flight' covers main aspects of aerial locomotion by birds including sections on history of science, aerodynamics, functional morphology, evolution, kinematics, physiology, energetics and costs of flight. The reader is expected to have some basic understanding of biology, physics and mathematics, but a university degree in any of these directions is not required. This book aims at a wide range of readers interested in the relationships between form and function. It should attract the attention of both professional ornithologists and amateur bird watchers. It is also aimed to be of interest to anyone preoccupied with the miracle of flight in general or with man made flying machines in particular. Equations, models and complex technical details are presented in separate boxes, studying the contents of these is not required to follow the main flow of arguments and information.

Common and scientific names follow Dickinson's (2003) 'The Howard & Moore complete checklist of the birds of the world'. Only common

names are used in the text. Appendix 1 lists these in alphabetical order with the accompanying scientific names; Appendix 2 provides the scientific names alphabetically with the associated common names. Biological terms are explained (mainly using the eleventh edition of Henderson's dictionary, 1996) in Appendix 3.

My personal interest in this topic was raised in the early 1960s by a book entitled 'De vliegkunst in het dierenrijk' (The art of flight in the animal kingdom) written by E. J. Slijper (who was my professor in zoology at the university of Amsterdam) in collaboration with the aero- and hydrodynamicist J. M. Burgers of Delft Technical University. More than twenty years later studies on the flight performance and energetics of common kestrels, in collaboration with the ecologist Serge Daan and his group (Groningen University, the Netherlands) and the aerodynamicist Daniel Weihs (Technion Haifa, Israel), offered the opportunity to actually contribute to the field. Kestrels and rough-legged buzzards kept as falconry birds for scientific studies made me an addict to the subject for the rest of my life.

There are many reasons why bird flight is fascinating. An important one is the fact that, as I hope to show, we don't fully understand how birds actually do it. Many features specific to the way birds behave during take-off, in flapping or gliding flight and during landing are still enigmatic. The movements are usually so fast that these must be studied in slow motion to appreciate what is actually happening. The study of the events inside flying birds is even more difficult. Another important reason for our lack of understanding is the problem that we are unable to see or measure the reaction of the air as a bird moves through it. So, there is still a veil of mystery over the interaction between bird, air and gravity, let us find out how far it can be lifted.

Watching a great variety of birds with special attention for the movements, helps to learn more about the flight mechanisms but it also emphasizes the feeling that we have a long way to go before we will fully understand avian flight. The background knowledge offered in this book is intended to make such observations even more rewarding. The following section gives an example of the kind of experiences I am aiming at.

Bird flight watching

The beauty, the variety and fascinating easiness of bird flight can be observed almost everywhere, however some places are better than others. My work as a marine biologist brings me every year to my favourite spot while teaching a field course in the marine life of Mediterranean rocky shores. I am privileged to be lodged at La Revellata lighthouse high on a cliff at the end of a rocky peninsula, overlooking the Bay of Calvi on Corsica, the island of beauty. It is a focus point for migrating birds, but there are also many residents breeding on the steep cliffs or hiding in the rich maquis vegetation. There is a large variety in species and sizes, from the tiny Marmora's warbler to the osprey,

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but it is not so much this type of variety that strikes me most. Every species shows different flight techniques, even those that seem to match closely in size, shape, and behaviour. This is demonstrated by the following personal impression of the variety of flight behaviours observed one morning from that vantage-point.

The fishing ospreys use flapping flight predominantly. The amplitude of the wing beats is shallow and it sometimes looks as if there is a snap in the middle between the hand and the arm part. They came earlier this morning soaring, using the upward movement of the sea wind obstructed by the high rocks of the peninsula. Ospreys are among the largest birds that are able to windhover. Windhovering is flying against the wind at the speed of the wind. They use it while fishing, remaining briefly at one spot above the water before diving into the water with the wings half closed. Ospreys make a peculiar shaking wing beat just after they take-off from the surface obviously to get rid of the water trapped between the feathers. It usually takes several strikes before a plunge is successful. The struggle in the water can be heavy. A bird with a fish in its claws wildly flaps its swept back hand wings while attempting to get out of the water. Once airborne, the fish is kept in an aerodynamically favourable head on position. Even with a fish, the ospreys can circle in up-draught without a single wing beat, the wings kept stretched with separated primary feathers, quickly gaining height up to well above the lighthouse before gliding down in the direction of the nest.

There are three falcons on the peninsula. The kestrels typically windhover, flapping the wings while keeping the head in a remarkably fixed position. They also make good use of up-draughts, enabling them to hang motionless on one spot. I am not sure if Eleonora's falcon breeds here, but they pass regularly causing havoc among the songbirds. The flight is impressive. The tips of the hand wings point backwards, while the dark grey birds shoot like slender arrows past cliffs and rocky outcrops. They never windhover. The peregrines that are nesting on the steep cliffs are more robust and bigger than the other two species of falcon. Hunting starts with circling high up in the air where they await a chance to stoop down on their prey at tremendous speed. The flight of the three falcon species could hardly be more different.

Two species of gull can be spotted on the small island rock just offshore from the lighthouse. The Audouin's gulls only occasionally show up. Apart from the red beak with black band and the dark green feet they look similar to the abundant yellow-legged gulls. These have yellow beaks with a red dot. The Audouin's wings appear slightly more slender than those of the yellow-legged gulls. Both species make good use of favourable wind conditions for soaring and gliding around the rocks. They spend hours effortlessly sailing the wind. From my high position I can observe the flight from above, the side and below. Gulls can glide absolutely motionless with stretched arm wings and swept-back hand wings. Their body is beautifully streamlined and looks small with respect to the wings. Sometimes they change to slow flapping flight with stretched wings, easily rowing. The Audouin's gulls forage in a typical way by flying against the wind very closely over the water

its position and its claim on the area. The way back up goes often in stages and in silence.

A spotted flycatcher perches in the top of last year's 4–5 m high dry flower stem of an agave. Its attitude is very alert and it dashes away on a quick flight excursion only a few metres away from the perch. This snap and return feeding strategy is typical for flycatchers all over the world. There will be differences in details of the flight kinematics but the general pattern is remarkably similar.

Marmora's warbler is very abundant here; it perches and sings in the highest branches of the small shrubs and bushes of the maquis. From there it makes nervous short flights or actually jumps with a short flutter of the wings from one perch to the next probably to establish and advertise its territory. It seems to forage by creeping over the vegetation looking for invisibly small insects. When alarmed these warblers fly over distances of up to a few hundred metres in a very condense type of bounding flight. This consists of a few high frequency wing beats followed by a short flight upward with the wings closed. It looks less regular and stable than the bounding flight of the European goldfinches. These migrants fly in a steady cadence clearly gaining speed during fast wing beats followed by a distinct bounce upwards. It is the steady pattern of a galloping horse. The closely related Eurasian siskin again flies similar but different. I could sit here for ages watching the variety in flight skills.

Bird flight watching brings strong impressions of the huge diversity in flight techniques. Each of these keeps the bird aloft but how? It seems hard to believe that there is one common principle. This book tries to summarize the knowledge about the various aspects of avian flight. Its purpose is to increase the interest in this aspect of bird life and to unveil our ignorance.