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Elected FRS 1990

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Colin Pennycuick was almost single-handedly responsible for the successful, and continuing, merger of the engineering and mathematical sciences of aerodynamics and flight mechanics with ornithology, ecology and bird flight behaviour. He developed a mathematical/ aerodynamical/ecological model of bird flight that could explain and predict bird body and wing shapes and sizes, and hence flight behaviour over a broad range of length- and time-scales, for real birds. He sought to bring rigorous quantitative methods to the people, and insisted that no matter how complex and sophisticated a theoretical model may be, unless it showed some improvement and advance in its practical utility, then it was of questionable value. He similarly insisted that model predictions be testable, and that results be openly and quantifiably given. His approach was marked by two distinct characteristics: first he pioneered the use of small aircraft and powered and unpowered gliders to follow soaring and migrating birds in their natural environment, exploiting his top-level pilot skills; second, he invented, designed and built novel instrumentation for making hitherto unheard-of laboratory and field measurements. The most well-known were his tilting wind tunnels, in which birds and bats could be trained to perform steady gliding flight. His intellectually and geographically-broad range of interests and contacts led to his being a giant influence in theoretical and practical bird flight mechanics and behaviour, one that is likely to stay with us for many decades.

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Early life

Colin James Pennycuick was born on 11 June 1933 to Marjorie and Brigadier James Alexander Charles Pennycuick in Windsor, Berkshire. His father joined the Royal Engineers in 1910 and served with some distinction in the 1914–1918 war, successfully blowing up a bridge in 1914 to save the British Expeditionary Force on their retreat from Mons in France.

At age five Colin flew over Singapore harbour, creating a vivid impression of life as seen from the air. Colin was educated at Lanesborough Preparatory School (1943–1947) and Wellington College (1947–1951), where he acquired a taste for bird watching and photography. He went up to Merton College, Oxford, to read biology (1951–1955), where he acquired a first in natural sciences and a Christopher Welch Scholarship in 1955. In 1953 he enlisted as Aircraftman Second Class Cadet Pilot in the Oxford University Air Squadron, graduating to Pilot Officer in 1955 and Flying Officer in 1956. During this time he flew de Havilland Chipmunks, a general purpose two-seater aircraft that became known for its aerobatic capabilities.

University education, RAF and postdoctoral studies

While at Merton, in 1954 Colin joined an expedition to Spitsbergen, which is an island north of Norway in the Arctic; this and a subsequent visit formed the basis of his first two publications on Brünnich's guillemots *Uria lomvia* and on arctic fulmar *Fulmarus glacialis* (1, 2). From a steep cliff observation point (figure 1), the soaring behaviour on cliff or wave faces could be traced (3). Successful flight requires reliable orientation and navigation systems, and Colin wrote an early paper (4) on how this might be achieved, sparking a lively discussion in the pages of *Nature* (5, 6) (see A1 and A2 in the online supplementary material for more detail of this work).

Colin completed his undergraduate degree in 1959 and then spent three years earning his PhD in the zoology department, Cambridge, under the supervision of Professor J. W. S. Pringle (FRS 1954). A series of four papers came from this work (7–10) (see A3 in the supplementary material), with the overall goal of examining the properties of frog muscle as an electromechanical system. The mechanical properties of muscles vary considerably according to loading conditions, cyclic usage and contraction rates. The experiments from Colin's own ingenious electromechanical apparatus to investigate them were novel, but it proved difficult to generalize.

Following award of his PhD in 1962, Colin took a postdoctoral position at the animal behaviour lab in Madingley, Cambridge, and has described how he trained pigeons to home on a mobile loft, which he would transport tens of kilometres in any direction to test their homing performance (62). Though the pigeons successfully adapted to loft movements, it taught him nothing about navigation other than their quick learning abilities to work out where they should go given any disruption.

The Bristol years I (1964–1968)

In 1964, Colin began a long association with University of Bristol as a lecturer. He built his next pigeon loft on the rooftop of the zoology department, and began some investigations (11,

Figure 1. Expedition to Spitzbergen, 1956. The meaning of the term 'steep cliff' in the text is clarified in the photograph on the right. (Reproduced courtesy S. Pennycuick.) (Online version in colour.)

12) that themselves homed in on what would become his tour de force, the measurement of flight performance from experiments in his custom-designed and built wind tunnel. The lineage of muscle performance study continued and, observing that the usual muscle performance estimates (multiply a mass (simple) by the average estimated power per unit mass (not at all simple)) were rather approximate, he estimated an upper strength limit by measuring the breaking strength of the muscle attachment and a lower limit from startle-response climbing performance of his tame pigeons. The window of muscle performance was not outlandish, with reasonable safety factors. If muscles are the engines, then we may regard the bones as the transmission and Colin examined the bone strengths in the pigeon wing, comparing them with likely loads based on simple stripwise aerodynamic calculations along the wing planform (12). He found that the safety margins, or load factors, were about the same as for gliders in current use and also reported that the implied lift coefficient in mid downstroke in hovering flight would be about 3.4, which greatly exceeded the lifting performance of known wings and airfoils at equivalent speeds and size.

The Bristol wind tunnel and basic aerodynamic measurements

The flight of insects and birds has long entranced earthbound humans, and the original impulse to embark on aeronautical adventures was clearly inspired by these living proofs of concept (cf. Anderson 1997). Early pioneers, such as Marey (1874) and Magnan (1934), had shown intricate details of the wing motions and sometimes of the resulting airflow too, but these and all subsequent studies of animal flight did not have control over the air. Just as the Wright brothers capitalized on systematic tests from their own wind tunnel, so Colin Pennycuick realized that such a platform was required for systematic and rigorous study. So he built one,
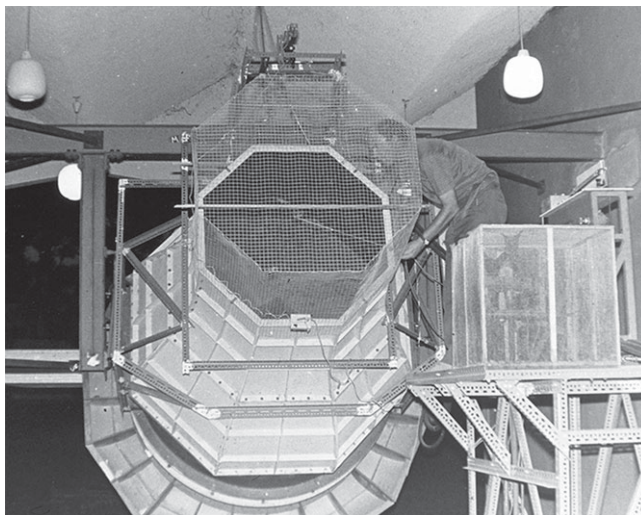
Figure 2. The Bristol wind tunnel. A bird in training sits on the end of a temporary perch. (Photograph by Colin Pennycuick; reproduced courtesy S. Pennycuick.)

and was the first to use wind tunnel data and observations to construct an aerodynamic model of bird flight.

Colin's custom wind tunnel was designed through programs developed on the first computer at University of Bristol. There were certain key elements of the design that were adapted to its use in animal flight studies. First the tunnel was open section, with a blow-through design. A test subject could be reached and cajoled to fly without great disruption to the airflow, and if the flight went wrong, the destination would not be in the fan blades downstream. Second, the entire apparatus could be tilted. This is an unusual feature, but is critical if gliding flight is to be studied. Gliding in an airstream arriving at some incidence angle is physically identical with gliding at that descent angle and flight speed through still air. Finally, the entire apparatus had to be compact so as to fit in a stairwell in the department—the only space available (figure 2).

Gliding flight is, in principle, much simpler than flapping flight, but had never been studied in this fashion (see further details in A4 of the online supplementary material). From an aeronautical point of view, and that of a glider pilot, it is the obvious way to investigate the aerodynamic foundations of free flight. The 'free' is emphasized here because, unlike their insect counterparts, birds (and later bats) would not and could not be attached to a tether. A series of landmark papers described the results of the wind tunnel studies and placed them in a theoretical framework (13–15) that was entirely new to bird flight. Since the experimenter has control of both the flight speed, U, and the incidence angle of the air, γ (determined by the tilting of the wind tunnel), then for a given weight W of the test subject, it is rather straightforward to estimate both lift and drag as

$$\left. \begin{array}{l} L = W \cos \gamma \\ D = W \sin \gamma \end{array} \right\}, \tag{1}$$
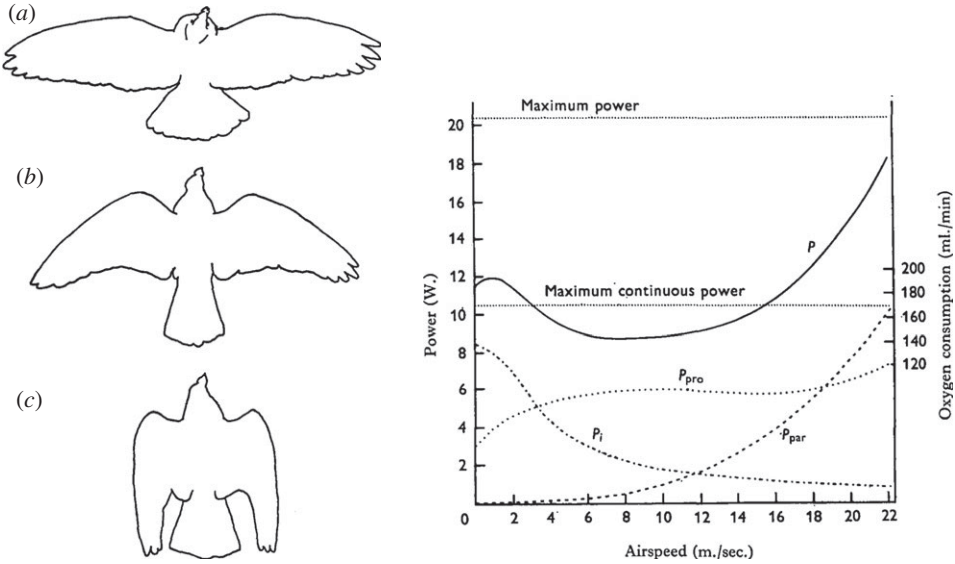
Figure 3. Two images from the first wind tunnel study of bird flight: (a) demonstrates the wing planform changes in a gliding pigeon from slow speed (top) to high speed (bottom); (b) is the first power curve estimated for bird flight. There is a pronounced minimum in the flight power required. (From (14), reproduced with permission from The Company of Biologists Ltd.)

and then the aerodynamic force coefficients are

$$\left.\begin{aligned} C_{\mathrm{L}} &= \frac{L}{qS} \\ C_{\mathrm{D}} &= \frac{D}{qS} \end{aligned}\right\}, \tag{2}$$

where $q = 1/2\rho U^2$ is the dynamic pressure, ρ is the air density and S is a reference wing area. Equations (1) and (2) show immediately how the proper experimental design, where for the first time γ is a known control variable, leads to estimates for the lift and drag coefficients and their ratio, L/D, which is commonly used as a measure of flight efficiency in aircraft. It is important to note that these wind tunnel observations were not just exercises in applying aeronautics to birds, but were informed and guided by the knowledge and intelligence of an experienced bird-watcher. Colin was well aware of the numerous postures and geometries of the wings, body, tail and feet that were used in practice (as pre-figured in earlier work (3)), which is why he knew to look for systematic variations with flight speed (and glide angle, γ). The pigeon silhouettes shown in figure 3 have been reproduced and discussed many times over and remain an instantly recognizable part of his unique imprint in the field.

The primary purpose of the wings is to generate the aerodynamic lift force, L, that supports the weight, W. The aerodynamic cost of this appears as the drag, D, which slows the aircraft down or requires it to descend at some angle—when this angle is equal to γ, the flight is in equilibrium and the speed is constant. Human-engineered aircraft have engines that provide sufficient thrust to overcome this drag, and then steady and level flight is possible. All the

glamour of flight is associated with lift, though it is actually the drag that is important in determining engine thrust, and hence fuel consumption. This remark applies equally to birds and planes. Lacking separate engines, birds produce both lift and thrust by flapping their wings, and careful selection of flapping amplitudes and wing pitch and trajectory allow them to also proceed in level or climbing flight. In fixed wing aircraft, the total drag is often written as

$$C_D = C_{D,0} + C_{D,i}, \tag{3}$$

where $C_{D,0}$ is a constant, determined by the viscous and pressure drags on the body, and $C_{D,i}$ is an unavoidable drag component that varies with C_L. The drag forces (in N) are then

$$D = qSC_{D,0} + qSC_{D,i}. \tag{4}$$

In slow flight, as U decreases, then equation (2) shows that C_L must increase, and therefore so does the induced drag, D_i, and its coefficient $C_{D,i}$. The dynamic pressure, $q \sim U^2$, and the consequence is that the first term on the right hand side of equation (4) increases with U, while the second term decreases. There is an optimum, intermediate speed when D is minimized, and this is the speed at which flight should occur. For any given flight mission, flight at the lowest D consumes the smallest amount of fuel. Colin noted that, from the point of view of the bird and its musculo-mechanical system, the power requirement is also of great importance. The power, which is the rate of doing work per unit time, can be expressed as $P = DU$, and Colin identified three components of the power required for flapping flight:

$$P = P_{par} + P_{pro} + P_i. \tag{5}$$

The components P_{par} and P_i are the same as the drag terms in equation (4) multiplied by the flight speed. The new term, P_{pro}, is required to account for the new drag cost of flapping the wings. Further details are given in A4 of the online supplementary material, but one of the main conclusions was that not only is there a speed at which total fuel consumption is minimized (the minimum drag speed), but there is another, lower speed when the fuel consumption per unit time is minimized.

The implications and application of the flight theory

The existence of optimum flight speeds, and different ones for minimum power versus maximum range, opened up a whole new frontier in avian biology with strong implications for migration and foraging behaviour. In these ground-breaking papers, Colin also outlined some of the ecological consequences, including the effect of size on the power required, and the power available for flight. Here we find the first quantitative argument for a maximum size or weight for a flying bird, as the flight capabilities of hummingbirds, vultures and condors are considered. The limits are ultimately set by surface area to volume ratios, as the wing surface area that scales as a length squared (or l^2) must support masses that increase as l^3. These arguments were elaborated in some detail, and he noted that, while practical birds may weigh up to 15 kg, those able to fly at a maximum range speed would be further restricted to about 6 kg and below (15).

Geese and swans are large birds that migrate successfully using flapping flight (the whooper swan *Cygnus cygnus* can weigh up to 15 kg) and the implication was that their aerodynamics must be more efficient somehow. In this respect it is noteworthy that Colin was at the time developing active contacts and collaborations at the Slimbridge Wildfowl and Wetlands Trust (WWT; founded by Sir Peter Scott, who was also a champion-calibre glider pilot). At the

time of its founding, and for many years after, the appearance of migratory geese and swans at Slimbridge was a somewhat mysterious phenomenon. Colin's calculations increased the depth of the mystery a little more, and his association with WWT remained active for many years, culminating in a widely-consumed BBC Radio 4 programme in 2008 where the movement of Speedy, the greater white-fronted goose *Anser albifrons*, tracked a close path to Colin's Cessna 182 while his performance was compared in real-time against predictions from the flight model.

NAIROBI AND THE SERENGETI (1968–1973)

In 1968 Colin moved to take a post as lecturer in the zoology department at the University of Nairobi, Kenya. In 1967 he had visited the Serengeti Research Institute in neighbouring Tanzania, and data from East African birds featured prominently in his work (15). His flight of a Slingsby T31 (which he described as a 'dreadful' aircraft) into the Serengeti that year was the first glider flight in Tanzania. He discovered that local dust devils could be reliable sources of thermal lift and that this brought him into shared airspace with a large flock of white storks. The drag on the glider was high enough to bring the overall aerodynamic performance more or less in line with that of the storks, and the adventure of flying side-by-side with the birds was born.

When taking up his lecturer position in Nairobi, Colin had brought his wind tunnel along, which he strung between acacia trees, and he also bought a Piper PA-12 Cruiser for the princely sum of £400. His new colleagues were initially sceptical, but the Cruiser soon became an essential instrument for touring around ecological study sites in Kenya, where rudimentary landing strips cut from the bush were quite common. All the elements were in place: a wind tunnel for controlled experiments, a glider for following soaring birds and a reliable powered transport for visiting and understanding the ecosystem as a whole. It remained to convert glider tracking experiments to quantitative data, so Colin invented a procedure for estimating relative speeds (both horizontal and vertical components) of the bird with respect to the glider, and then deriving for the bird a glide polar by reference to the known performance characteristics of the glider itself (a Schleicher ASK-14 with the canopy removed and a custom camera and range-finder mount in front of the pilot).

THERMAL SOARING IN VULTURES

In November 1970 Colin submitted three manuscripts to the *Journal of Experimental Biology*: one from glider-based observations of the African white-backed vulture *Gyps africanus* in free flight (18), one on the aerodynamic properties of Rüppell's griffon vulture *Gyps rueppellii* from drag measurements of a specimen mounted in the wind tunnel (19), and one on the gliding flight of the dog-faced bat *Rousettus aegyptiacus* observed in free gliding flight in the tunnel (20).

The glide performance measurements were analysed in some detail (18) so as to construct a glide polar where the sink speed is plotted as a function of forward speed. The polar reconstructions were not completely straightforward, as corrections had to be made for the scarcity of data at low forward speeds and high-lift coefficients. Two constants were involved in the fitting of an aeronautically-consistent curve to the data: a span efficiency factor, k, and

a parasite drag coefficient, $C_{D,0}$. The simple form and subsequent analysis is made possible by these constants, but establishing their value is something of a dark art. The experimental relationships established by Colin can be used to investigate and/or establish likely lower and upper bounds, and many of his works in subsequent years took aim, in one way or another, at these aeronautical quantities. Colin also introduced (18) a question that remains a source of enquiry, and sometimes dispute, today and can be paraphrased as: why do vultures not look like albatrosses? He showed that a vulture equipped with albatross aerodynamics ought to fare better in almost all cases, with the possible exception of very tight turns in small thermals, and, although explanations for the characteristically splayed wingtips at the end of rather blunt wing tips are often advanced on grounds of aerodynamic efficiency, the real reason must have something to do with take-off and landing performance and constraints, and not purely aerodynamics.

Flight with a wing membrane

The first aerodynamic experiments on a gliding bat built upon a careful examination of the musculoskeletal and wing system (20). Bat wings are formed from an elastic wing membrane stretched between elongated digits of the modified hand, and the tension in the wing membrane supports and transmits the aerodynamic loads to the body. If the tension is released, then the membrane will balloon out into a non-useful shape and at worst will flap uselessly like a flag. Bats therefore do not show the same wing planform adaptations to varying speeds as birds, and glide over a reduced speed range. By contrast the profile section shape at any cut through the wing in the streamwise direction did show significant variations that were consistent with the known and unusual aerodynamic characteristics of airfoils at small scale (where, for example, rough or sharp edges can improve performance by promoting early transition to turbulence), and were also consistent with requirements for stability in tailless aircraft. The observations of wing geometry were made using a pair of stereo-cameras, and these photographs would later be analysed in quantitative fashion using photogrammetric reconstruction techniques (26) (figure 4). Fifty years later there have been no better, or even further such measurements of bats in steady gliding flight.

Quantitative observations from a glider

From 1971 to 1973 Colin was installed as deputy director of the Serengeti Research Institute. A successor to the old Piper Cruiser was used by up to 50 pilots working the area, and Colin undertook a number of investigations on broader ecological studies, inventing new measurement techniques from aerial platforms and making quantitative analyses of all kinds of animal movements. The Serengeti and surrounding rift valley were sites for movements of immense herds of ungulates as they followed the availability of water and food over large ranges. Their predators had smaller available range and were thus obliged to lead a more episodic lifestyle with times of feast and lean pickings.

   The motions and intersections of these groups of animals comprise an important component of the ecosystem as a whole, and Colin continued to observe and measure from his plane and powered glider (figure 5); 304 hours of flight observations of East African birds were described (21) in flight performance with respect to the ASK-14, and in general movements following the large ground-based populations, which are described as a food supply. His remarkable paper, published in 1972 (21), contains lengthy natural history-type descriptions of the region and the birds in it, which are then followed by a quite technical analysis and discussion, based
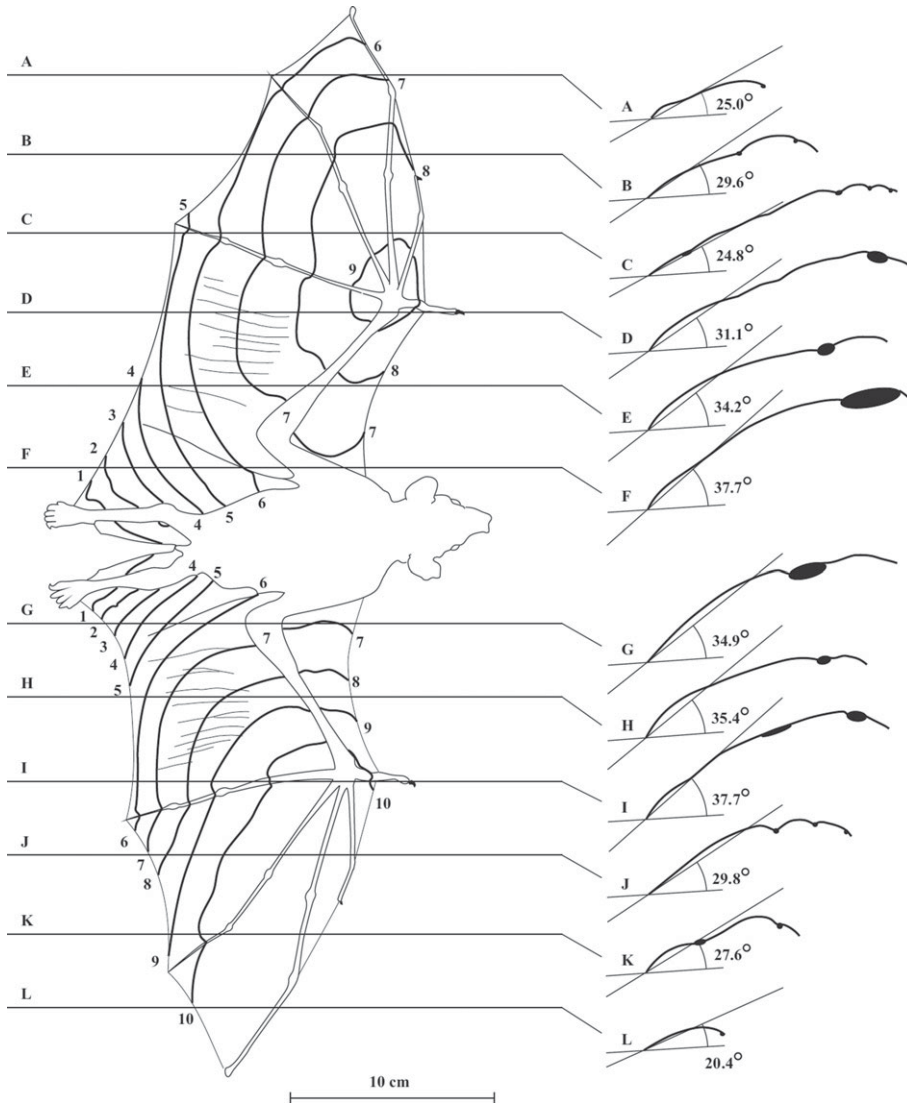
Figure 4. The three-dimensional geometry of the bat wing membrane in gliding flight. (From (26), reproduced with permission.)

on the theoretical developments of the likely glide polars (14, 15, 18) and the relative cost of soaring and flapping flight in large and small birds. The ability to think of the natural world from these differing viewpoints and to synthesize them is uncommon. From the beginning, Colin was determined that all mathematical and theoretical treatments should in the end be about the animal, and should be usable and useful to all studying them. In this spirit, his paper on the flight of vultures (27) is an equation-free summary of the East African studies.

Figure 5. Sandy, Colin Pennycuick's wife, entitled this picture 'Colin in his element'. (Reproduced courtesy S. Pennycuick.)

Aircraft make excellent platforms for surveys of animal populations as well as fellow gliding or soaring birds, and a consistent thread in Colin's work is to use photography and careful error analysis to convert images to quantitative data. Several papers show examples of the efforts to find the correct scale and orientation of photographic instruments (16, 22, 24, 29), and optical methods were proposed to guide and estimate the height of an aircraft from ground, a necessary first step in then being able to quantify the data (23). Aerial census data were gathered for pelicans and flamingos (24, 25) and interests in the flamingo were extended to a quite detailed energy budget calculation made possible by the predictable behaviour and feeding mechanism (a constant flow rate filtering pump for extracting blue-green algae from alkaline lakes). When and if sufficient algal concentrations occur, then the flamingos may breed, but these conditions are local and variable, which explains the nomadic lifestyle.

Previous observations of white-headed *Trigonoceps occipitalis* and lappet-faced vultures *Torgus tracheliotus* (21) showed a more sparse distribution than their *Gyps* sp. counterparts, and one that did not move about following prey concentrations. Rather, these two species have very low wing loading ($Q = W/S$ where W is the weight and S the wing surface area) that allows them to operate in weak thermals and efficiently stay aloft, at the expense of cross-country speed. By staying local and flying early, they can be first at a kill, where they must soon compete with hyenas and other later-arriving vultures. The distribution of these two species (30) reflects this feeding–nesting–breeding cycle that is itself a measure of secondary productivity, and, since the nesting density is quite amenable to aerial census, the variation of this productivity can be inferred also. Understanding the flight behaviour as part of the overall ecosystem dynamics was also reflected in studies on facial markings in lions (17) and on the running mechanics of ungulates (29) (see A5 in the online supplementary material).

On his return migration to England, Colin outfitted the Piper Cruiser with an extra 55-gallon fuel tank, parked on the seats normally occupied by passengers. He flew from Nairobi to Cairo (narrowly avoiding the initial rumblings of the 1973 Yom-Kippur war as he drew up next to a huge Antonov in his little Piper) to Crete and thence to England, where he re-took a position as lecturer.

THE BRISTOL YEARS II (1973–1983)

After returning from Africa in 1973, Bristol became his home base for a decade and Colin started and became involved in a number of research projects on bird flight. He was promoted to reader in 1975.

The ornithodolite and the flights of seabirds

In the late 1970s Colin developed the ornithodolite, a direct descendant of the device he had invented earlier (3). The ornithodolite is a portable, computer-based instrument used to measure flight speed of birds on short time-scales (33). An optical range finder, azimuth and elevation axes were all fitted with custom Gray-code discs for LED-photodiode arrays to convert the information to eight-bit binary form and input into a parallel port on an early portable computer. A local anemometer was read for estimates of wind speed, and then each tracking operation, following a target bird, yielded the three-dimensional trajectory and then local heading and airspeed.

The first field study using the ornithodolite was made during an expedition to Bird Island, South Georgia, from 1 December 1979 to 23 February 1980 (figure 6), and on the expedition ship *RRS Bransfield* to and from South Georgia. The results from this expedition, comprising about 9300 observations from the previously non-field-tested device, were published in a seminal paper in *Philosophical Transactions of the Royal Society B* (34), detailing the observations of flight speed and behaviour in seabirds, ranging from the 38 g Wilson's storm petrel *Oceanites oceanicus* to the 9 kg wandering albatross *Diomedea exulans*. All albatrosses and the giant petrel *Macronectes* sp. were found to almost never flap their wings whenever even trace winds were active, making progress through slope soaring or flying in and out of ocean waves in a zigzag pattern. As Colin noted in his analysis of the gliding flight of the fulmar petrel (3), dynamic soaring theories of quite some sophistication had been developed but did not seem to have been closely followed by the actual birds, who instead used a mix of local wind shear and up-wave slope soaring, extracting energy from the complex and shifting wave and wind field.

When slope soaring over Bird Island, the albatrosses would fly slower than predicted (for either minimum power or maximum range) and with statistically significant numbers of occasions with high estimated lift coefficients that must have been made possible by unsteady (time-varying) effects and special wing performance from controlled separation, made possible by drooped leading edge contours. The paper (34) also reported the discovery of a mechanical lock in the shoulder joint of the albatross wing, significantly reducing the muscle work required to extend the wing during gliding flight; and for performance at sea, a quite conservative calculation showed that a fuel fraction of 1% body mass in the wandering albatross would carry it for about 1000 km over 29 hours, without flapping its locked wings. The interesting conclusion was reached that larger birds were better suited for long range due to this shift from flapping to soaring flight. One does not reach this conclusion using the standard range equations for fixed wing aircraft, where range is independent of size.

The next application of the ornithodolite was during a field trip to Flamenco Island, Panama, from 21 May to 6 June 1980, where three large, dissimilar species using thermal soaring were observed to test predictions about climb rate and circling radii in relation to wing loading (35). Here Colin revisited the question about why bird wing shapes are as they are (18), now based on quantitative data for the frigatebird *Fregata magnificens*, brown pelican

Figure 6. Colin Pennycuick with sooty albatross (a) and ornithodolite (b) on Bird Island, South Georgia. (Reproduced courtesy S. Pennycuick.) (Online version in colour.)

Pelecanus occidentalis and black vulture *Coragyps atratus*. The longer, pointy wings (with high *AR*, *b*; recall equations (3) and (4); figure 7) allow the frigatebird to remain airborne day and night, but take-offs from the ground or water surface are not possible. By contrast, the broader slotted-tip wings of the vulture and pelican allow for such manoeuvres. Both frigatebird and vulture reached lift coefficients of 1.6 in slope soaring. Such values are not
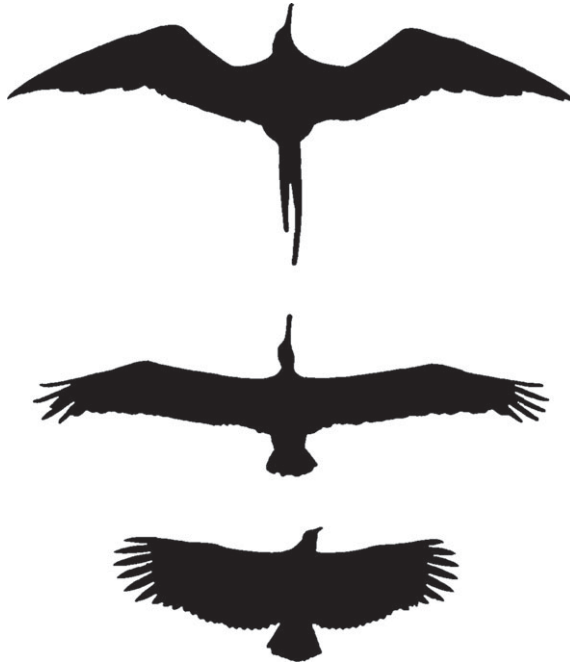
Figure 7. Silhouettes of a frigatebird, brown pelican and black vulture, drawn by Colin Pennycuick from video. This image has provoked many to wonder why wing shapes are the way they are. Some answers are suggested in his work from which this image was extracted. (Reproduced from (35) with permission from The Company of Biologists Ltd.)

attainable in standard trimmed wings without auxiliary high-lift devices such as flaps and slats.

A third expedition was made in the summer of 1986 to Foula, Shetland, where Colin recorded flight tracks of northern hemisphere seabirds over 11 days. Measurements of 11 species were made, including auks, skuas, gulls, gannet *Morus bassanus* and shag *Phalacrocorax aristotelis*. By comparing flight mode and lift coefficients with those previously obtained from South Georgia (34), Colin made inferences about the interaction between speed selection, flight mode and wing shape (39).

These three expeditions and the papers stemming from them generated a very powerful synthesis of novel instrumentation, careful error and quantitative analysis, and application of the emerging flight modelling work to understanding and predicting how real birds work. An example of ornithological outcomes of the data and theory combined (37) showed how scaling arguments of flight costs and requirements of food provisioning to the growing chick(s) could be used to develop a quantitative ecological theory of foraging radii and growth rate in petrels and albatrosses.

The flight theory

In these years Colin was recruited to write a review on bird flight for the scholarly book series *Avian biology* (Academic Press). What emerged instead was a 75-page opus entitled

'Mechanics of flight' (28), where Colin developed the first complete version of his general flight model, including extensive diagrams and tables for the calculation of flight ranges of birds given only body mass, wing span and fuel ratio. The chapter also discussed the power available from flight muscles, and the scaling of flight performance with body size in regimes of flapping, gliding and soaring flight. This book chapter is likely the most widely read account of bird flight ever written, and it has served as an inroad to the complicated field of animal flight mechanics for generations of scientists and students.

In October 1977 Colin participated in a conference on bird migration research, held at Falsterbo, Sweden, and his unorthodox contribution 'Fifteen testable predictions about bird flight' (31) was published in the journal *Oikos*. This paper, a direct extension of the book chapter (28), was where Colin worked out quantitative predictions on various aspects of flight performance and physiology, all derived from flight mechanics. In the paper Colin noted that 'the theoretical basis of our understanding of bird flight is somewhat rudimentary at the time of writing, but could be considerably improved if each experimental or observational project were designed from the outset with the intention of testing some specific prediction from theory'. In his characteristically clear and crisp language, it was also a gentle but firm reminder of the inutility of performing what he termed theory-free investigations.

To Sweden

During the conference in Falsterbo in 1977, Colin and Thomas Alerstam (one of the conference organizers) made plans to study the spring migration of common cranes *Grus grus* by combining ground-based observers, surveillance radar, goal-tracking radar and direct observations from an aircraft (the Piper PA-12). The airplane was piloted by Colin with co-pilot Alerstam making notes on a map. The cost of flapping flight scales as $m^{7/6}$, becoming considerable in larger birds, both in terms of energy requirements and demands on the musculoskeletal system, and, since common cranes are relatively large birds at 5–6 kg, one would expect they would find ways to reduce flight costs.

In spring, common cranes depart from the Rügen peninsula in northern Germany and cross the Baltic Sea by flapping flight, but when entering over land on the Swedish south coast they revert to cross-country soaring flight. Cranes gain height by circling in thermals and then convert the potential energy into forward distance. However, unlike storks, that almost exclusively glide between thermals, cranes extend their inter-thermal flights by bursts of wingbeats interspersed with gliding. Cranes also maintain nicely ordered formations both when circling in thermals and during the partially powered glides between them. By comparing the observations of the cranes' flight performance against alternative predictions (31), it was inferred that by pursuing a hybrid flight strategy, involving flapping flight in cross-country soaring, cranes reduced the energy cost of travelling. It was further argued that powered flight is the primary mode of flight in common cranes, and that cross-country soaring represents a more advanced flight mode (32).

Home base and testing theory

Colin's flight theory was simple and hence practical, a stunning example of the possible success in the art of engineering approximation to difficult problems in biology. Some of these approximations were huge; there was no real accounting for the fact that flapping wings only slightly resemble an infinitely thin disc that (somehow) accelerates air downwards, and there was no way to include any of the geometric and kinematic details of the wingbeats themselves.

In the late 1970s Colin assembled a small group of PhD students, K. D. Scholey (KDS) and Geoffrey R. Spedding (GRS), and a postdoc, J. M. V. Rayner (JMVR), who had arrived fresh from having completed his own major works on the theoretical basis of flapping flight (Rayner 1979a, b, c). They worked on theoretical models of flapping wing aerodynamics (JMVR), on measurements of actual air motions created by birds in flight (GRS) and on the detailed kinematics of the wingbeat cycle (KDS). Further details are in the online supplementary material (A6), but suffice to say that these efforts and their descendants continue to this day as the community looks to maintain the balance between realism and simplicity that was making the existing flight model so effective.

Colin, of course, could not be purely laboratory-based and he was busy renewing contacts with the WWT Slimbridge group while continuing to attend to glider operations. The field expeditions included a trip with KDS to the Paracas peninsula, Peru, to observe and film the soaring flight of condors and turkey vultures *Cathartes aura* along the coast and up the side of the Andes (36). The Andean condor *Vultur gryphus* is large and heavy (wingspan b up to 3.2 m, and mass 11–15 kg for fully-grown males), and almost certainly cannot easily fly at minimum power speeds, relying instead on predictable winds and slope soaring to commute between nesting and feeding grounds. The observed behaviours and dependence on ambient wind were consistent with the analysis and predictions, and it is remarkable that a heavy bird, so reliant on weather patterns, is viable.

Consideration of the high power requirements of slow flight leads to a conundrum: how did flight ever start if the costs of getting off the ground are so formidable? Colin's flight mechanical arguments naturally lead to a number of apparent constraints and feasible scenarios about how flight could have evolved, not only in birds, but in insects, pterosaurs and bats, too. Though it was not a major focus of his work, the flight mechanical arguments could not be ignored, and Colin advanced detailed arguments (38) on the possible nature of proto-membranous wings, the development of flight in pterosaurs and bats, and the feathered wings of later birds. Certain of these threads are discussed in A7 in the online supplementary material.

MIAMI, THE CARIBBEAN AND SOUTH AMERICA (1983–1992)

In 1982, the migratory impulse again took hold, and Colin was appointed as the second holder of the Maytag chair of ornithology at the University of Miami, Florida, which now became a new home base for nine years, 1983–1992. Miami was nicely-located for explorations to central and south America, to the Caribbean and to various southern States. Here he continued to publish results based on field campaigns in the Shetlands, but he also initiated new field studies of the flight performance in birds with the aim of testing predictions from his earlier theory (31).

Estimating drag and other elusive quantities

During the Miami period Colin coordinated a number of wind tunnel studies and experiments involving dead and captive birds. The first (42) was an effort to measure the body drag, D_{par}, which has a similar form to the first drag term in equation (4),

$$D_{par} = qSC_{D,par}, \tag{6}$$

and is not easily measured, depending on exact details of the surface texture and body geometry. Though in principle easier to estimate than D_{pro} of the moving wings (cf. A8), its accurate estimate raises formidable challenges, particularly at the size and speed range of birds. The size l and speed U of a moving object combine with the density ρ, and viscosity μ, to form a dimensionless number, the Reynolds number:

$$Re = \frac{\rho U l}{\mu}. \tag{7}$$

When Re is the same, the balance of forces between inertial terms and viscous terms in the governing fluid dynamical equations is the same, and Re in Colin's paper (42) was reported as $1.5–4.6 \times 10^5$. Towards the lower end of this range, especially, estimating drag of even simple bodies is challenging. The overall goal was to provide coefficients $C_{D,par}$ so that a library of values could be established for different body shapes (and for different Re at lower Re). Colin and his team duly mounted frozen (dead) and wingless bird bodies on a drag balance, using medium to large sized waterbirds and raptors. The library was compiled and used as defaults in the flight model calculations, but major uncertainties remained concerning the applicability of dead-body measurements to the in-flight case, even more so when one includes the modified background flow due to the action of the wings, whether or not they are flapping.

At around this time it was becoming popular to deploy radio transmitters on birds, typically attached as a back-pack harnessed above and between the shoulders. Perhaps anticipating the boom of using satellite transmitters in avian biology (1990 and onwards), Colin and his collaborators measured the potentially detrimental effects to the bird of carrying such devices. It is not only the addition payload that increases the flight cost, but the additional aerodynamic drag penalty may be much worse, depending on the streamlining of the transmitter (40, 43). During the experiments it was noticed that some feathers on the back of the dead bird bodies fluttered in a way that was not seen on live birds, indicating that the flow separates from the body. By applying hair spray to prevent the feathers from fluttering, the measured drag coefficient was reduced by 15%. Ever since this experience, in addition to arguing against the use of radio transmitters (59), Colin also argued against the utility of measuring dead birds in wind tunnels, since he believed the results were not good enough.

While in Miami, Colin acquired a Cessna 182 and a 6.7 m Helson sailboat for further explorations and field studies. One of his PhD students in Miami, F. Schaffner, worked on the biology and energetics of white-tailed tropicbirds *Phaethon lepturus* breeding on a small island about 30 km east of Puerto Rico. As a part of the study, tropicbirds were equipped with radio transmitters (a tail-mounted configuration was the least disruptive) and could be tracked by plane to their off-shore foraging locations up to 176 km away from the colony (46). The field metabolic rate was measured by the doubly labelled water method, suggesting the birds carrying radio transmitters had significantly increased metabolic rates, although they had similar foraging success and food provisioning rates to the young as birds without radios. Since tropicbirds feed by plunge diving, it may be unsurprising that the total metabolic costs increase with a transmitter attached.

A number of field campaigns involving ornithodolite measurements were carried out at various locations in the continental USA, including from the sailboat in the Everglades, Florida, which introduced a new method to estimate the lift to drag ratio (*L/D*) from combined measurements of flight speeds and video recordings of the wingbeat kinematics. The new analysis exploited the finding that the wake disturbance of a bird in cruising flight seemed

to consist of a continuously undulating wake with constant strength (Spedding 1987). In that case the main asymmetry in the down- and upstrokes of a wingbeat cycle required to produce a net positive thrust was produced just by having a reduced span on the upstroke. The wing is otherwise loaded continuously, operating at the same effective lift coefficient.

Given this model system, Colin then realized that the drag could be simply related to the ratio of span extension in the down- and upstrokes (44), so he measured these in double-crested cormorants, *Phalacrocorax auritus*, filmed from close to head-on as they left their mangrove island roost to feed. *L/D* calculated from the span-ratio analysis came out to be around 15, a quite respectable number for a flying device at this scale. It is also higher than a value of 9, which would have been predicted by default settings on the flight model; something was wrong somewhere. Plausible variations in various constants and parameter values in the flight model could not close the gap, and it was noted that the flight model estimates, if based on too low a value of *L/D*, would then predict too high a value of the mechanical flight power required, *P*.

Wings that flap

As may be expected from the search for correct drag coefficients, there is plenty of room for error and refinement in all the components of *P* in equation (5), and the studies described in this period took aim at each one in turn. In particular, Colin made a number of efforts to account for the fact that bird wings actually flap. One approach was to compile a database of flapping frequencies and amplitudes, and this is what Colin did (45). The exercise (detailed in A9 in the online supplementary material) yielded a handy formula from which the wingbeat frequency could be predicted for any unknown bird, given its mass, wingspan and wing area. This kind of result was important because very often an ornithologist wishing to generate predictions from the flight model would not have all the data required, so the model, combined with a database of careful and verified measurements, is the key to its success in the field.

Flight: the software

During the Miami years Colin continued to amend and extend his flight mechanical model through wind tunnel studies, and he also made an effort to popularize the flight model by publishing the landmark book *Bird flight performance: a practical calculation manual* (44), which was accompanied by a five-inch floppy disk in a pocket on the inside cover. On the floppy disk were simple programs written in Visual Basic that could be run as is, using defaults and the databases compiled and/or verified by the author, or they could be modified to taste. The broad distribution and transparency of the methods and data behind the predictions was a turning point in the reach of bird biology, paving the way for a wide audience to introduce themselves and their students to the productive interface between biomechanics, physiology and ecology. In new editions, the disk shrank to 3.5 inches, and ultimately the software moved to a web-based platform. The program was called *Flight* and it was carefully maintained, nurtured and updated over the years. The last official book that explicitly centred on *Flight* was a very extensive update in 2008 (57). It can be found on the bookshelves of amateur ornithologists and professional aerospace engineers, and has had as profound an influence as any publication in bird flight.

Before leaving Miami to move back to Britain, Colin had the Cessna modified to carry 400 L of fuel (the range of a bird and of an aircraft depends on the fuel fraction) and took off on the homeward migration, with first stopover in West Greenland (figure 8). Here, Colin helped

Figure 8. Colin and Cessna *ca* 1992 on his migration from Miami to the UK via Greenland and Iceland, a track that was later followed by Speedy, the Greenland white-fronted goose. (From (62), used with permission from the Pennycuick family.) (Online version in colour.)

American colleagues to track radio-tagged Peregrines *Falco peregrinus* for a few weeks before setting off on 4 August 1992 from Kangerlussuaq, across the Greenland inland ice and Denmark strait to arrive at Reykjavik, Iceland, after a 6.5-hour nonstop flight. From Iceland he finally arrived in Bristol after an impressive solo flight, sub-divided into multiple flight steps and stopover interludes, much as the birds carry out their own long-distance migration. Bristol would become his base for the rest of his life.

The Bristol years III (1992–2015)

Upon his third arrival in Bristol, Colin became an associated research professor at the Department of Zoology, and promptly married Sandy (with whom he co-authored his last publication) and settled into his new/old home base of Bristol. Colin's version of settling did not exclude continued explorations of bird migrations, as he renewed connections with WWT at Slimbridge and also embarked on an extensive collaboration with Lund University, Sweden.

A new wind tunnel at Lund

While still in Miami, plans for a novel wind tunnel specially designed for experiments with live birds were already underway, and these took more concrete form as he plotted with Thomas Alerstam at Lund. An engineering company based in Sweden, Rollab AB, and its chief engineer, John Rosén, were engaged in the design plans, which resulted in a document to form the foundation of a grant application. A private research foundation, the Knut and Alice Wallenberg foundation, judged the application favourably and decided to provide the necessary monetary resources for the new wind tunnel. At the time, Lund University was constructing a new building for the ecology department, and, thanks to an economic depression and decreasing construction costs in its wake, an annex to the new

ecology building could be accommodated within the original budget. Both the housing and the tunnel were ready in the autumn of 1994, marking the start of a new era in animal flight studies.

The tunnel design made use of lessons learned in the early Bristol experiments (13). Three critical features were: 1) a blow-down configuration with open-ended test section for introducing and training test subjects; 2) a tilting mechanism so either steady climbing or gliding flight could be investigated; and 3) low turbulence levels, typically <0.05% of the mean freestream, the importance of which was beginning to be more clearly understood. The technical specifications were documented in detail (50), also something of a first.

Wingbeat frequencies and further estimates of drag: what could be wrong?

At first, the instrumentation was sparse, but Colin's understanding of the steps needed to encourage steady and reliable flights led to early well-controlled flights, and, in keeping with the attention on real wingbeat kinematics, a flap-o-meter was designed to measure wingbeat frequencies. The flap-o-meter consisted of a rotating plastic cylinder with four opposing holes through which the bird could be observed, and when the wings appear motionless, the frequency of the rotating holes matches the wingbeat frequency. The wingbeat frequency of two species (a thrush nightingale *Luscinia luscinia* and a teal *Anas crecca*) was measured and showed a parabolic relationship with airspeed, with a clearly defined minimum in each case (47). Based on Colin's earlier arguments (28), the speed for minimum $f(U)$ ought to coincide with minimum power speed, but they did not, as predicted values from the flight model were only about two-thirds of the observed speeds and the birds were very reluctant to even fly at the predicted speeds. Again, something was wrong, and attention turned to the various parameters in the flight model, and in particular the body drag coefficients that had hitherto been obtained from dead bodies mounted in wind tunnels of various kinds. If $C_{D,par}$ were reduced by more than a factor of four, from default values of 0.4 to 0.08, then the kinematic data and model predictions matched. There were already reasons to suspect drag data, such as from Colin's work on large waterfowl and raptors (42), so the default value in the flight model was duly adjusted downwards.

A central theme in Colin's research had been to predict the power required for a bird to fly and then to use empirical measurements to refine the flight mechanical theory (14, 28, 31, 44, 48, 51, 57). In viewing high-speed videos of a swallow *Hirundo rustica* flying in the Lund wind tunnel, Colin noticed that the body bobbed up and down in phase with the wingbeat. Since the mass is known, the vertical acceleration gives the vertical force applied by the wing at the shoulder joint, and, by measuring the moment arm and angular velocity of the humerus from the videos, the work done by the flight muscle could be estimated. The work done per unit time (dividing the cycle total by the wingbeat period) is another independent estimate of mechanical power (53). Estimating power in this way yielded higher values than if calculated from the theory using the now-standard body drag coefficient $C_{D,par} = 0.1$, while $C_{D,par} = 0.26$ matched the measurements. More recent estimates from visualizations of the wake in a jackdaw *Corvus monedula* suggest that $C_{D,par}$ is likely near 0.2 (Klein Heerenbrink *et al.* 2016), and considering the ornamental tail streamers of a swallow a value of $C_{D,par}$ above 0.2 seems at least possible.

Incessantly chasing elusive drag coefficients in different conditions is an unsatisfactory process that may not necessarily converge. Measuring precise quantities in animal flight is not easy, and if we suppose an optimum, trimmed, minimum drag condition for any given speed,

then any departures will draw estimates away, often to higher inferred values of aerodynamic constants, which themselves may not necessarily be constant. When and if a flight model informs us about the natural ecology, then it can be said to be useful, even if not an unreachably 100% accurate. Colin realized all this, of course, and the wind tunnel experiments devised to test various elements of the flight equations were conducted while much broader field expeditions were also in play.

Long-distance migration

In the broad spectrum of flight behaviour, ranging from assisted hops between tree branches to critical tests of range or endurance, it is in long migrations with their fixed purpose and incentives for fuel economy that we may expect to find the most strict adherence to a model that predicts a strategy to optimize over available parameters, such as course selection, wingbeat frequency and flight speed itself. The advent of satellite-based tracking systems with small(ish) transmitters allowed continuous monitoring of certain predictable migrations, first involving the whooper swan migrating between Iceland and Britain (49) (see A10 of the supplementary material). The swans were found to select flight conditions consistent with using a visible horizon for navigation (52). Optimal strategies and conditions change during the course of a long flight as fuel is consumed and the mass decreases accordingly, and changes were made to the *Flight* program so that incremental variations could be included step-by-step as a long flight progressed. The program was successfully deployed in tracking and describing the flight of the bar-tailed godwit *Limosa lapponica baueri* over 11 000 km flights from Alaska to New Zealand, and of the 5420 km spring migration of the greater knot *Calidris tenuirostris* from Australia to China (55).

Although it is important to understand that there is no aerodynamic magic at play, such feats are extraordinary to behold, and a successful radio programme on the BBC, *World on the Move*, followed three different species of geese as they travelled north from their home base in Slimbridge to Greenland, Iceland and then Spitzbergen (see A11 in the supplementary material). The track through the equations of the flight model was followed simultaneously with their tracked progress, and it was noted that there seemed to be strong incentive to arrive on time or early at a destination, when the richest food rewards would first be available (58). This emphasis on speed over fuel economy mimics in some respects the scheduling and operation of commercial passenger transports.

It is tempting to draw such analogies with our human-engineered systems, and with other modes of locomotion in nature: how do the costs of flight compare with those of swimming, or running? To address such a question, a rational measure must be defined, and a dimensionless cost of transport can be expressed as

$$C_\mathrm{t} = \frac{P}{WU}. \tag{8}$$

P is the power required for transport (overcoming all resistive forces) at speed *U* for a device with weight *W*. Over all human-engineered systems, C_t is highest for flight, but flight is the only way to achieve high speeds (Gabrielli & von Karman 1950). The lowest costs are incurred by ships, where *W* is supported with no effort. Similarly in the animal kingdom, C_t is lowest among comparably sized animals for swimming, highest for running and then intermediate for flying. C_t for all locomotion decreases as size increases, so covering ground (or water) over a reasonable time seems to favour large- or medium-sized birds. Colin considered such transport

Figure 9. Colin was happiest when in the field, following his passions. Here he is looking completely content while sitting on the side of a hill in Iceland in 1995. (Photograph by Sverrir Thorstensen.) (Online version in colour.)

costs, and, being careful to account correctly for various chemical–mechanical conversion efficiencies, invented a performance number, which is otherwise the reciprocal of C_t (41, 56). Further detail is given in A12 in the online supplementary material.

The last migrations

One of the enduring objectives of Colin and his flight model was to predict and understand flight and migratory strategies of birds and to frame the speed and trajectory selection in overall ecological context. An underlying assumption is that body shapes, sizes and behaviour are strongly selected for energetically efficient solutions, for high N, but that variations due to ambient winds and turbulence, and to other physical and ecological imperatives (does the male plumage look good to the female?), can be expected to occasionally trump the model imperatives (e.g. (48, 51); Hedenström & Alerstam 1995). As good quality measurements accumulated over species, so the instrumentation has improved. The range finder in the ornithodolite was replaced with a Vector, a high-quality pair of 7×42 binoculars with built-in laser range finder, a magnetic compass and an angular elevation sensor and deployed in two studies at bird migration hotspots in southern Sweden, Falsterbo and Ottenby. The data served as a basis for evaluating the consequences on optimal flight speeds of bounding flight and tail wind (54) and, inevitably, the effect of body size on migratory flight speed (60).

Towards the end of his working life, Colin's movements became slightly more localized, but he and his VW camper van were frequently spotted in the cargo bay of the Lund wind tunnel, at whooper swan catch sites in Iceland (figure 9) and, of course, at the WWT Slimbridge. He continued to write in direct and thought-provoking style (61) and his last publication (62) was a book, co-authored with his wife Sandy, documenting his years following the birds, from the East African years onwards.

Overall assessment

Colin Pennycuick was a singular individual, who revolutionized the study of flying birds in a way that is unlikely to be repeated. His pioneering field studies in small planes and gliders, his novel wind tunnel constructions and experiments, his formulation of a flight model that was just complicated enough to claim to be based on physics, but simple enough to actually be used, his continued invention of new instrumentation and, finally, his democratization of his research by reaching out to all communities through clearly-written manuals to freely-distributed computer codes, are all significant achievements. Together, the scope and influence is hard to circumscribe. For many years, his life and travels read like a *Boy's own* comic book, but in real life, and throughout that life, he maintained a youthful enthusiasm that was infectious and stimulating. He was rigorous and, when it was appropriate, mathematical in his thought, but he was always fair, ready to abandon ideas when faced with contradictory evidence and ready to listen to new ones. Perhaps owing to these characteristics, his work has often spawned more questions than answers, and generations of researchers will find inspiration in the pages of his articles, and in his books (see A13 of the online supplementary material).

Colin Pennycuick has had a lasting and indelible impact on the academic community, and on those simply fascinated with birds. We offer this memoir partly as an accounting of some of this influence and partly in the hope that it will further inspire more inquisitive and curious minds.

Awards

1955   Christopher Welch Scholarship, Merton College, Oxford
1978   Corresponding Fellow of the American Ornithologists' Union
1983   Maytag Professor of Ornithology at University of Miami
1990   Fellow of the Royal Society
1996   Honorary Doctorate, Lund University

Additional material

Additional material relating to the life and work of Colin Pennycuick is supplied in an online supplement, which is available at https://doi.org/10.1098/rsbm.2021.0023. This contains Appendices A1–A14, which provide more detail on his research, information about his published works and some examples of his appealing writing style.

An extended version of this memoir can be found at http://ame-dept.usc.edu/docs/spedding/CJP-Obit-bioRxiv.pdf.

Acknowledgements

Author profiles

Geoffrey Spedding

Geoffrey Spedding took his undergraduate degree in Zoology at the University of Bristol in the years 1975–1978. In his second year of study, he took a course in Animal Mechanics, taught by Colin Pennycuick. Here we learned why elephants do not look like scaled-up versions of mice, why all animals run at the same speed, and why birds are, in fact, helicopters. These exciting and novel ideas completely transformed his career trajectory, and in 1978 he began a PhD under CJP's supervision, on the aerodynamics of bird flight. The PhD was finished in 1981, and he moved to the University of Southern California for postdoctoral studies with Tony Maxworthy, on mechanical models of insect wings. Surrounded by exotic experiments on geophysical fluid dynamics, he acquired a taste for tightly controlled, quantitative experiments in fluid flows and has worked on them ever since. CJP was responsible for his eventual re-surfacing in the biology world and made introductions to the Lund University group. The Lund wind tunnel had just been completed, and he and co-author (AH) worked together on new, quantitative experiments on bird and bat flight. All the while CJP was coming and going, keeping a watchful eye, enthusiastically (and patiently) awaiting developments and outputs. The collaborations and our enthusiasm, stemming from his, continue to this day.

Anders Hedenström

Anders Hedenström took his BSc in Biology at Lund University, Sweden in 1990, and started his PhD trajectory on the ecology of bird flight in the same year under the supervision of Thomas Alerstam. The starting point was Colin Pennycuick's 1975 book chapter on 'Mechanics of flight' in *Avian Biology*, where, based on aerodynamic principles in combination with optimality reasoning, he had developed theory about flight and migration strategies in different ecological contexts. It was during these years that CJP became a regular visitor to Lund, both for field projects with his ornithodolite and his Cessna 182, and to make plans for a new wind tunnel dedicated to animal flight research. After postdoctoral studies in Cambridge with Charlie Ellington FRS, he returned to Lund University to start his own research programme on animal flight and migration with the then new wind tunnel as main infrastructure. CJP was a regular visitor until 2015, which was not only a great inspiration, but also yielded tangible outputs (50, 53). This work continues to this day with the aim of improving models of migration strategies and to link flight mechanics and flight metabolism. In September 2012, CJP and his wife Sandy came to Öland, Sweden, to install a new ornithodolite. This was during the migration season and two weeks of intense field work resulted in a research paper (60). The collected work of CJP will remain an inspiration and immediate point of departure for many years to come.

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