Fuel economy in cross-country soaring flight

C.J. Pennycuick

School of Biological Sciences, University of Bristol, Woodland Road, Bristol BS8 1UG, United Kingdom.

Not published, but used in the Glide Polar section of the *Flight* program, to calculate chemical power in gliding flight, and effective lift-to-drag ratio in cross-country soaring

Abstract

The pectoralis muscle in large soaring birds is subdivided into a large superficial part and a smaller deep part. The deep part is thought to be a specialised (slow) tonic muscle that holds the wings down in the horizontal position in gliding flight. If the superficial part provides the power for flapping flight, then its maximum strain rate would have to be adjusted to generate maximum power at the shortening strain rate in flapping, which can be calculated, and the deep part would have to be capable of shortening at the same strain rate, without necessarily exerting any force while doing so. This would allow the maximum strain rate of the tonic muscle to be lower by a factor of 0.28 than that of the fast power muscle, and its rate of consumption of fuel energy in an isometric contraction can be calculated on that basis. This is added to the basal metabolic rate to estimate the total rate at which the bird requires fuel energy in gliding flight. The additional fuel energy required for occasional wingbeats during gliding flight can also be calculated and added. A form of effective lift-to-drag ratio, based on the cross-country speed, is used to estimate the fuel used per unit distance of cross-country flight. These calculations have been incorporated as enhancements to the Glide Polar calculation in the author's published *Flight* program, so that the fuel energy requirements of a soaring bird that is tracked by a data logger or satellite transmitter can be determined.

Introduction

Most small and medium-sized birds flap steadily along when migrating, but large birds, apart from some notable exceptions such as swans and bustards, depend to varying degrees on soaring. The most usual method by which large birds migrate long distances is by

repeatedly climbing in a thermal, and then using the height gained to glide in the required direction. The average cross-country speed in such a climb-glide cycle is less than that in straight flapping flight, because no horizontal progress is made during the climb. The technique is familiar to glider pilots and is described in a slightly simplified form by a theory attributed originally to Paul MacCready, and presented in many books on gliding, such as Welch et al. (1977). The achieved cross-country speed, as calculated from the MacCready theory, depends strongly on the rate of climb in thermals, and less strongly on the selected gliding speed between thermals.

Considering muscles as engines, as in Chapter 7 of Pennycuick (2008), represents a point of view that is familiar from aeronautics, but somewhat different from the usual physiological perspective. Horizontal flight requires mechanical work to be done by an engine (the flight muscles in birds), and the power, or rate at which work is required from the muscles, is basically the drag times the forward speed. Subject to some modifications to accommodate flapping wings, this idea is used by my *Flight* program to predict the *mechanical power*, that is the rate at which the muscles have to do work in level flight. The *chemical power*, or rate of consumption of fuel energy, is derived from the mechanical power, taking account of the efficiency with which muscles convert fuel energy into work, and adding in some overheads, especially basal metabolism. The same program also predicts the cross-country speeds of birds migrating by thermal soaring, from the standard MacCready theory, but up to Version 1.20, it said nothing about energy consumption in this case, because no mechanical power is required for gliding flight. Drag is overcome by consuming potential energy (losing height) instead of by muscular work. However, soaring flight is not as "effortless" as some observers imagine, because a soaring bird requires a steady tension in the muscles that hold the wings in the horizontal position, balancing the wing-root bending moment. Some expenditure of fuel energy is needed to maintain this tension, even though the muscles do no external work.

This paper introduces a method for calculating the chemical power required to hold the wings level in gliding, which can then be added to a statistical estimate of the basal metabolic rate, to get an estimate of the total chemical power required by a gliding bird. This power can be combined with the cross-country speed from the MacCready theory to estimate the *effective lift-to-drag ratio* (or effective L/D) in cross-country soaring. This version of the effective L/D determines the distance covered per unit of fuel energy consumed, over a series of climb-glide cycles, and corresponds directly to the effective L/D for flapping flight, which is calculated for the same purpose in the *Flight* program's simulation of flapping migration.

The effective L/D, when combined with the notion of *energy height* (Pennycuick, 2003), provides a simple way to calculate a bird's *range*, that is the distance it can fly for a given amount of fuel.

Anatomy of the pectoralis muscles

In all birds, the two pectoralis muscles (left and right) contract together to pull the wing down in the power stroke of flapping flight, but in large birds that are specialised for soaring, such as vultures, storks and albatrosses, each pectoralis muscle is subdivided into a large superficial part and a smaller deep part (Kuroda, 1961; Pennycuick, 1972). When the superficial part is removed in dissection, the deep part is revealed, lying along the angle where the dorsal plate of the sternum joins the keel, and itself covering the supracoracoideus muscle, which elevates the humerus. Usually, the superficial part is deep red in colour, while the deep part is pale pink, indicating that, while both are aerobic muscles, the superficial part is capable of oxidising fat at a higher mass-specific rate than the deep part. The following power calculation is based on the hypothesis that the superficial part is the engine, which converts fuel energy into mechanical work in flapping flight, and is specialised to deliver maximum power at the reference frequency for horizontal flight (below), while the deep part

is a tonic muscle, specialised to exert a steady downward moment on the humerus in gliding.

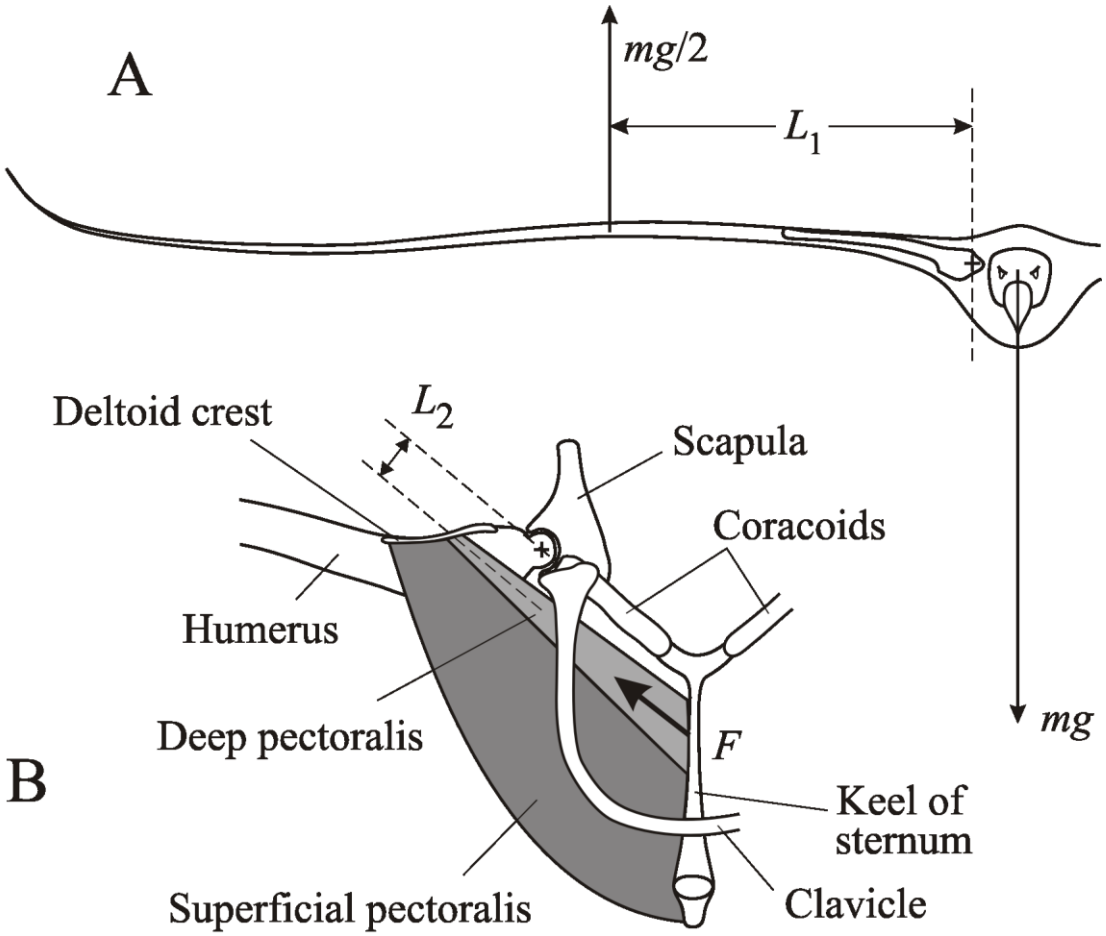


Fig. 1. A. Each of a gliding bird's wings supports half the weight (*mg*). The lift acts through a point at a distance L_1 from the shoulder joint, exerting a moment $L_1mg/2$, which has to be balanced by an equal and opposite moment applied to the humerus by the pectoralis muscle.
B. The deep part of the pectoralis of large soaring birds (pale grey) is believed to be the tonic muscle that continuously applies a force *F* to the deltoid crest of the humerus, through a line that passes at a distance L_2 from the shoulder joint. The moment FL_2 balances the lift moment. The superficial pectoralis (dark grey) is believed to be the engine in flapping flight, adapted to deliver maximum power at the wingbeat frequency.

Chemical power for tonic muscles

Fig. 1A shows how the lift on each wing of a bird in straight, unaccelerated gliding flight supports half the weight (*mg*), and acts through a point which is displaced outwards from the shoulder joint by a distance (L_1), which is typically about 40% of the semi-span, or 20% of the wing span. The moment tending to rotate the wing upwards around the shoulder joint is therefore $mgL_1/2$, where *m* is the body mass, and *g* is the acceleration due to gravity.

This moment has to be balanced by an equal and opposite moment from a steady force F exerted by the deep part of the pectoralis muscle, acting at a moment arm L_2 about the shoulder joint (Fig. 1B). The steady force (F) required from the tonic muscle is

$$F = (mgL_1/L_2) / 2. \quad (1)$$

It has been known for many years that the rate at which a muscle requires fuel energy to maintain a given steady force is higher for a "fast" muscle than for a "slow" one. The power required by a muscle contracting isometrically (i.e. without being allowed to shorten) can be calculated from A.F. Huxley's (1957) model of the sliding filament mechanism of muscle. McMahon (1984) showed that this theory gives a good account of the experimentally determined properties of muscle, and also presented Huxley's equations in a form that allows the energy cost of maintaining an isometric force to be easily determined. The equations themselves are far from simple, but when they are combined to find the power required to maintain a steady force, without any external work being done, the following simple result emerges (Pennycuick 1991):

$$p_{ATP} = \sigma_{max}\, \psi_{max} / 16. \quad (2)$$

p_{ATP} (lower-case p) is the volume-specific ATP power, i.e. the rate at which energy is required from the dephosphorylation of ATP, per unit volume of the muscle. σ (Greek sigma) is the *stress* exerted by a contracting muscle, i.e. the tension force exerted across unit cross-sectional area of the myofibrils, and ψ (Greek psi) is the strain rate at which a muscle shortens, meaning that if one end of the muscle is fixed, ψ is the speed at which the other end moves, divided by the extended length of the muscle.

σ_{max} is the *isometric stress* that the myofibrils develop when the muscle is stimulated, but held at a constant length, and not allowed to shorten. σ_{max} is closely related to the maximum force that can be exerted by a single myosin filament. As the geometry of the filament array is essentially the same in all vertebrate skeletal muscles (H.E. Huxley, 1985), this isometric stress may be considered constant in all vertebrates. Observations of a very large bird (Whooper Swan) have been used to deduce that the value of σ_{max} cannot be less than 560 kN m^{-2}, and that is the default value used here and in the *Flight* program, despite somewhat lower values having been reported in the physiological literature (Pennycuick, 2008)).

ψ_{max} is the *maximum strain rate* at which a particular muscle is capable of shortening, if it is unrestrained, and exerts no force. ψ_{max} is the quantity that identifies a muscle as "fast" or "slow". It varies from one muscle to another, and can be adjusted in an individual muscle by adjusting the rate constants in A.F Huxley's (1957) molecular model. Its value has to be

matched to the load for which the muscle is adapted, for example the pectoralis muscles of small birds must have a higher ψ_{max} than those of large ones, so as to deliver maximum power at the right wingbeat frequency. It follows from Equation 2 that a tonic muscle, being specialised to maintain a steady force rather than to do work, must have the lowest value of ψ_{max} that can be reconciled with any shortening that is required of it.

Characteristics required of the pectoralis muscles

In flapping flight, the superficial (fast) part of the pectoralis muscle has to deliver maximum power while contracting at a wingbeat frequency which is constrained by the geometry of the wings (Pennycuick 1990, 1996). It has been shown in field studies of a variety of species that the wingbeat frequency in level flight at the minimum power speed is close to the "reference frequency" (f_{ref}), given by

$$f_{ref} = m^{3/8}\, g^{1/2}\, b^{-23/24}\, S^{-1/3}\, \rho^{-3/8}, \qquad (3)$$

where m is the body mass, g is the acceleration due to gravity, b is the wing span, S is the wing area, and ρ is the air density (Pennycuick 2001). f_{ref} is always available in the *Flight* program, as all five of the variables on the right-hand side of Equation 3 are required as user input. The exponents are not empirical, but follow from the requirement that both the left and right hand sides of Equation 3 have the dimensions of inverse time (T^{-1}). During flapping flight, both parts of the muscle must shorten through a strain (λ) in approximately half the wingbeat period, so that the strain rate (ψ_s) during shortening is

$$\psi_s = 2\, \lambda\, f_{ref}. \qquad (4)$$

The standard value of λ for locomotor muscles is 0.26, as this is the maximum that allows all crossbridges to be connected throughout the muscle's length range. If the fast muscle's maximum strain rate is ψ_{maxFM}, then the requirement that the muscle has to deliver maximum power when shortening at ψ_s means that

$$\psi_{maxFM} = \psi_s / 0.28. \qquad (5)$$

This follows from Hill's (1938) force-velocity relationship for a shortening muscle, and is explained in Pennycuick (2008). The tonic muscle's maximum strain rate (ψ_{maxTM}) needs to be as low as possible, to minimise its chemical power requirement (Equation 2). The lowest value that would allow the slow muscle to keep up with the fast one during shortening in flapping flight, without exerting any tension, is

$$\psi_{maxTM} = \psi_s, \qquad (6)$$

and this is the value that is used in Equation 2 to calculate the power requirement. It is conceivable that the ratio of the maximum strain rates could be measured in a laboratory experiment. If that could be done, the predicted result would be that $\psi_{maxTM} / \psi_{maxFM} = 0.28$.

Volume of the tonic muscles

With values assigned to σ_{max} and ψ_{maxTM}, the volume-specific ATP power required by the tonic muscles can be calculated from Equation 2. ATP is the immediate source of energy for the contractile protein machinery. To get the chemical power for a tonic muscle (P_{TM}), as measured by oxygen consumption, the volume-specific ATP power has to be multiplied by the combined volume of the left and right tonic muscles (v_{TM}), and divided by 0.6 for the 60% efficiency with which the mitochondria convert fuel energy to ATP energy.

$$P_{TM} = p_{ATP}\, v_{TM} / 0.6. \qquad (7)$$

It remains to estimate the volume of the muscles, in order to get the power itself from Equation 7. The geometry as shown in Fig. 1 constrains the moment (FL_2) that the muscle has to exert, but allows different combinations of origin area, moment arm and muscle length that would produce the required moment. However, in geometrically similar birds, one would expect the muscle volume to scale directly with the body mass, and in the absence of a direct way to calculate it, we have to resort to empirical methods. In the original description of the subdivided pectoralis muscles of African storks and vultures, Pennycuick (1972) found that the deep part accounted for 8-11% of the mass *of the whole pectoralis muscle*, but in a later study (Pennycuick, 1982) the deep part was found to be 6-15% of the whole muscle in petrels, but much higher (23-33%) in albatrosses. However, the pectoralis as a whole is a smaller fraction of the body mass in albatrosses. If the mass of the deep part of the pectoralis is expressed as a fraction of the body mass, rather than of the whole pectoralis muscle, a figure of 1.5% fits both groups reasonably well, given the doubtful condition of some of the specimens that were dissected. As a provisional expedient pending better data, we can estimate the volume of the tonic muscles for both sides (v_{TM}) as

$$v_{TM} = 0.015\, m / \rho_{musc}, \qquad (8)$$

where m is the body mass and ρ_{musc} is the density of muscle, for which the standard value is 1060 kg m^{-3}.

Chemical power in gliding and effective lift-to-drag ratio

Besides the chemical power for the tonic muscles from Equation 7, a gliding bird also (presumably) expends fuel energy for basal metabolism, so that the total chemical power (P_{glide}) can be represented as

$$P_{glide} = P_{TM} + P_{BMR}, \quad (9)$$

where P_{BMR} is the basal metabolic rate. All three terms in Equation 9 represent chemical power, i.e. rate of consumption of fuel energy. Unlike the power in flapping flight, whether mechanical or chemical, P_{glide} is not a function of speed, and remains the same whether the bird is circling in a thermal or gliding straight between thermals. This power can be combined with the average cross-country speed (V_{cc}) from the MacCready theory to create an effective lift-to-ratio (N) that refers to one or more complete climb-glide cycles:

$$N = m\,g\,V_{cc} / \eta\,P_{glide}, \quad (10)$$

where η (Greek eta) is the efficiency with which muscles convert chemical energy into mechanical work (default value 0.23 in *Flight*). η is not zero in this context, but just a conversion factor, introduced to make the chemical power in the denominator into an equivalent mechanical power (effectively drag times speed). This makes it directly comparable with the numerator mgV_{cc} (weight times speed), which has the dimensions of power but is purely mechanical. Being essentially lift times speed divided by drag times speed, N is the ratio of an average lift to an average drag, requiring no units. The significance of the lift-to-drag ratio (or "aerodynamic efficiency") for calculating range has been understood in the aeronautical world since the early days of aviation (Breguet, 1922). There was never any reason for later physiologists to introduce the inverse ratio as "Cost of Transport", still less to obscure its dimensionless nature, and its simple relationship to fixed-wing aerodynamics, by retaining the complicated combination of units from which they derive it.

Soaring with occasional wingbeats

Most or all soaring birds flap their wings occasionally during the inter-thermal glides, and a few, such as Common Cranes, use every intermediate from pure thermal soaring when conditions are suitable to continuous flapping flight when soaring is not possible (Pennycuick et al. 1980). The effect of sporadic flapping is to flatten the inter-thermal glides, so increasing the cross-country speed, at the expense of consuming some additional fuel energy. Although the *Flight* program only considers the ends of the spectrum, thermal soaring according to the MacCready model and continuous flapping flight, it is possible to take account of occasional

wingbeats in a bird that is being tracked by a GPS data logger or satellite transmitter. An accelerometer in such a device could be used as a wingbeat counter, and with this in mind, the Glide Polar output includes an estimate of the fuel energy required per wingbeat. It gets this by dividing the minimum mechanical power (for level flight at V_{mp}) by the reference wingbeat frequency from Equation 3, and then divides the resulting estimate of the work done per wingbeat by the conversion efficiency, to convert work to fuel energy. No allowance is made for basal metabolism in this case, since that is already included in the calculation of gliding power (Equation 9).

Scaling of chemical power in gliding

From Equations 2 and 7, the chemical power for the tonic muscles is proportional to the volume of the muscles (v_{TM}), the isometric stress (σ_{max}) and the maximum strain rate (ψ_{maxTM}). In geometrically similar birds these three variables would scale with the body mass (m) as follows:

$v_{TM} \propto m$ (proportional to m)

$\sigma_{max} \propto m^0$ (independent of m)

$\psi_{maxTM} \propto m^{-1/6}$ (same as wingbeat frequency).

Hence the chemical power for the tonic muscles is expected to vary with $m^{5/6}$. This is almost the same as the basal metabolic rate, for which the empirical scaling is usually near $m^{0.75}$, but much less steep than the scaling of mechanical power for horizontal flapping flight, which would vary with $m^{7/6}$ in geometrically similar birds. Consequently, energy saving by soaring is expected to be more effective in large birds than in small ones.

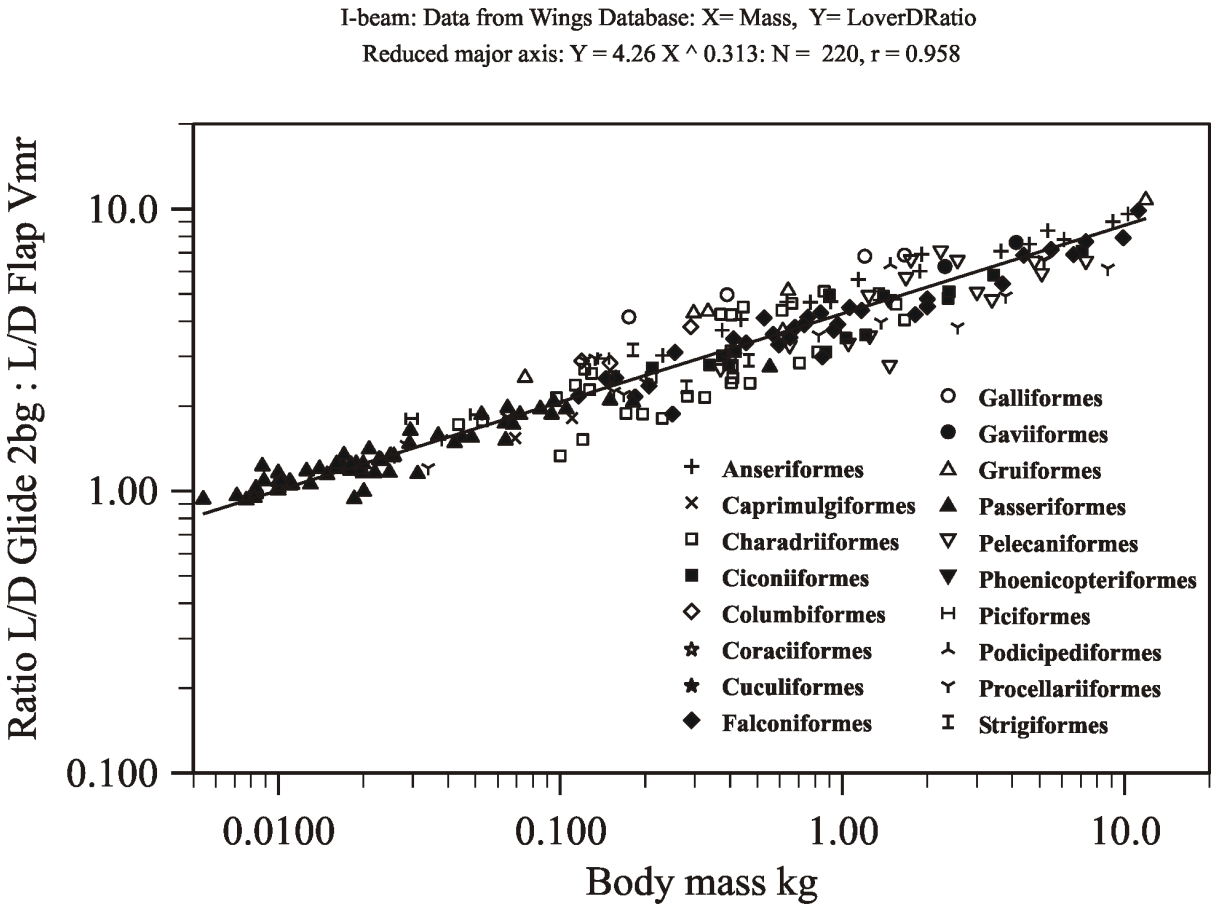


Fig. 2. Log-log plot of the ratio of two lift-to-drag ratios calculated by the *Flight* program for 220 species in the "Wings" database. They are the effective L/D for cross-country soaring in thermals giving a rate of climb of 2 m/s, flying at the speed for best glide ratio between thermals; and the effective L/D for level flapping flight at the maximum range speed (V_{mr}).

Scaling of effective lift-to-drag ratio in soaring versus flapping

The effect of wing allometry on speeds, powers and other quantities that can be calculated by the *Flight* program was examined at length in Chapter 13 of Pennycuick (2008). The method was to calculate some quantity for each of the 220 species in the program's "Wings" database, and then fit a reduced-major-axis line through a double-logarithmic plot of the results, with body mass on the X-axis. Fig. 2 shows such a plot for the ratio of two lift-to-drag ratios, for cross-country flight by thermal soaring versus flapping. From Version 1.21 of the *Flight* program, the effective L/D in cross-country soaring is tabulated in the MacCready table, in the Glide Polar output, and the value selected was for a rate of climb of 2 m s^{-1} in thermals, flying at best-glide speed between thermals. The Glide Polar output also now includes the effective L/D in flapping flight at the maximum-range speed for comparison, and the ratio of these two L/D estimates is plotted on the Y-axis in Fig.

2. The cluster of solid triangles at the left end of the diagram represents passerines, who would get about the same L/D by thermal soaring as by flapping (ratio about 1). As thermal soaring is only practicable in a limited range of conditions, and only in daylight, and also results in a lower cross-country speed than flapping, it is not an attractive option for most small birds. Small birds have ample muscle power to meet the needs of horizontal flapping flight, whereas increasing size makes this progressively more difficult, and many large birds appear to resort to soaring for this reason alone. However, Fig. 2 suggests that the vultures and swans at the right-hand end of the diagram can get a tenfold higher effective L/D by soaring than by flapping, meaning that for a given percentage of the body mass consumed as fat, these large birds can go 10 times further by soaring than by flapping. Each method has its advantages and drawbacks. Storks and eagles rely on thermals and need only modest fat loads for migration, but are restricted to the hours of daylight, and to routes and seasons where soaring conditions are reliable. Cranes leave Spain and cross the Pyrenees in thermals, but often end up flapping when they get to Sweden, while Whooper and Bewick's Swans accept the expense of flapping flight to reach their sub-arctic nesting grounds in time for the short high-latitude breeding season.

This theory is incorporated in the *Flight* program from Version 1.21 onwards. The program is available as a free download from the following websites

http://www.bristol.ac.uk/biology/research/staff/pennycuick.c.html
http://books.elsevier.com/companions/9780123742995

Acknowledgements

I am indebted to Rory Wilson and Emily Shepard for introducing me to their field studies of Andean Condors, for suggesting enhancements to the *Flight* program, and for helpful comments on a preliminary draft of this paper.

References

Breguet, L., 1922. Aerodynamic efficiency and the reduction of air transport costs. Aeronaut. J. 26, 307-313.

Hill, A.V., 1938. The heat of shortening and the dynamic constants of muscle. Proc. Roy. Soc. London B 126, 136-195.

Huxley, A.F., 1957. Muscle structure and theories of contraction. Progress in Biophysics and Biophysical Chemistry 7, 255-318.

Huxley, H.E. ,1985. The crossbridge mechanism of muscular contraction and its implications. J. Exp. Biol. 115, 17-30.

Kuroda, N., 1961. A note on the pectoral muscles of birds. Auk 78, 261-263.

McMahon, T.A., 1984. Muscles, reflexes and locomotion. Princeton University Press, Princeton.

Pennycuick, C.J., 1972. Soaring behaviour and performance of some East African birds, observed from a motor-glider. Ibis 114, 178-218.

Pennycuick, C.J., 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. Phil. Trans. R. Soc. London B 300, 75-106.

Pennycuick, C.J., 1990. Predicting wingbeat frequency and wavelength of birds. J. Exp. Biol. 150, 171-185.

Pennycuick, C.J., 1991. Adapting skeletal muscles to be efficient. In: Efficiency and economy in animal physiology. Blake, R.W. (Ed.) Cambridge University Press, Cambridge, pp. 33-42.

Pennycuick, C.J., 1996. Wingbeat frequency of birds in steady cruising flight: new data and improved predictions. J. Exp. Biol. 199, 1613-1618.

Pennycuick, C.J., 2001. Speeds and wingbeat frequencies of migrating birds compared with calculated benchmarks. J. Exp. Biol. 204, 3283-3294.

Pennycuick, C.J., 2003. The concept of energy height in animal locomotion: separating

mechanics from physiology. J. Theor. Biol. 224, 189-203.

Pennycuick, C.J., 2008. Modelling the Flying Bird. Elsevier, Oxford.

Pennycuick, C.J., Alerstam, T., Larsson , B.,1980. Soaring migration of the common crane *Grus grus* observed by radar and from an aircraft. Orn. Scand. 10, 241-251.

Welch, A., Welch, L., Irving, F., 1977. New Soaring Pilot, 3rd Edition. Murray, London.