ESTIMATING POWER CURVES OF FLYING VERTEBRATES

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Summary

The power required for flight in any flying animal is a function of flight speed. The *power curve* that describes this function has become an icon of studies of flight mechanics and physiology because it encapsulates the accessible animal's flight performance. The mechanical or aerodynamic power curve, describing the increase in kinetic energy of the air due to the passage of the bird, is necessarily U-shaped, for aerodynamic reasons, and can be estimated adequately by lifting-line theory. Predictions from this and related models agree well with measured mechanical work in flight and with results from flow visualization experiments. The total or metabolic power curve also includes energy released by the animal as heat, and is more variable in shape. These curves may be J-shaped for smaller birds and bats, but are difficult to predict theoretically owing to uncertainty about internal physiological processes and the efficiency of the flight muscles. The limitations of some existing models aiming to predict metabolic power curves are considered. The metabolic power curve can be measured for birds or bats flying in wind tunnels at controlled speeds. Simultaneous determination in European starlings *Sturnus vulgaris* of oxygen uptake, total metabolic rate (using labelled isotopes), aerodynamic power output and heat released (using digital video thermography) enable power curves to be determined with confidence; flight muscle efficiency is surprisingly low (averaging 15–18 %) and increases moderately with flight speed, so that the metabolic power curve is shallower than predicted by models. Accurate knowledge of the power curve is essential since extensive predictions of flight behaviour have been based upon it. The hypothesis that the power curve may not in fact exist, in the sense that the cost of flight may not be perceived by a bird as a continuous smooth function of air speed, is advanced but has not yet formally been tested. This hypothesis is considered together with evidence from variation in flight behaviour, wingbeat kinematics and flight gait with speed. Possible constraints on flight behaviour can be modelled by the power curves: these include the effect of a maximum power output and a constraint on maximum speed determined by downstroke wingbeat geometry and the relationship between thrust and lift.

Key words: bird, bat, flight, aerodynamics, power, vorticity, wingbeat kinematics, gait, efficiency, thermography.

Introduction

The 'power curve', which expresses the relationship between power consumption and air speed for a flying animal, has come to dominate the study of vertebrate flight. It is a convenient formulation for the performance of a flying animal and is valuable as a tool for comparing different flight patterns or behavioural strategies. Important insights into, for instance, decisions about flight speed or the optimum strategies for feeding and migration have been gained from theoretical analyses of the power curve (see, for example, Pennycuick, 1969; Rayner, 1990; Houston, 1992; Hedenström and Alerstam, 1995; Weber and Houston, 1997). None the less, power curves are surrounded by a considerable degree of controversy. In this essay, I review the mechanics and physiology underlying power curves, clarify some aspects of their definition and use recent measurements to validate some theoretical models for flight power.

There are a range of methods for determination of a power curve. Theoretical models offer the greatest flexibility, but the most direct method is to measure total energy uptake during flight in a wind tunnel at controlled speeds. These experiments have so far been applied to a limited range of species, and only recently has there been any attempt to validate alternative techniques; such measurements cannot readily be extrapolated from one species to another, and there must always be doubt about how close the controlled but possibly stressful conditions in a wind tunnel are to natural, free flight (see, for example, Rayner, 1994a). Mathematical models have been derived to predict power consumption as a function of flight speed (and also of other quantities such as climb angle and acceleration) and of bird morphology, and some of these are sensitive to wingbeat kinematics. Many authors have used such models to predict flight behaviour. The simplicity of application of some

of the models means that it is easy to ignore the assumptions implicit in the underlying theory. The nature of the model appropriate for any particular problem varies greatly according to the goal of the analysis. Sophisticated unsteady aerodynamic analyses may be required to understand the performance of flapping wings, to interpret patterns of wingbeat kinematics or to understand wake vortex development. At the other extreme, much simpler models based on fixed-wing aircraft and with diminished sensitivity to all aspects of aerodynamics may be sufficient for understanding behavioural decisions during flight.

Modelling flight power

Power consumption is modelled by partitioning the rates of energy flow that a bird or bat sheds into its environment. The energy rates involved can be large: empirically, total power consumption during steady, level, continuous flapping flight is typically 10–20 times basal metabolic rate. The evolution of morphological adaptations, of life history strategies and of flight physiology in birds and bats has been dominated by the high energetic demands of flight and the large mechanical forces in the wing and shoulder (for a recent review of flight evolution and aerodynamics, see Rayner, 2000). The starting point for estimating flight power is therefore to compute the mechanical or aerodynamic energy consumed during flight, which can be defined formally in two largely equivalent ways: (1) as the increase in the kinetic energy of the air caused by the passage of the bird, and (2) as the mechanical work performed by the flight muscles at the shoulder joint. Following the first definition, methods derived initially to model mechanical power output for low-speed aircraft can be applied to animals. The second definition recognizes that work is done during flight only by the muscles that flap the wings, and emphasizes the need to incorporate the considerable energy released as heat by the flight muscles as they generate mechanical work.

Models derived on this basis can provide reasonably accurate estimates of the aerodynamic work done during flight, but it is the *total* metabolic energy consumed that will have the greatest influence on flight and foraging decisions and on the evolution of life histories. The method used to estimate this quantity appears to have been described first by Marey (1890), but is most familiar from the model of Pennycuick (1968, 1969), subsequently modified or reformulated by Tucker (1973, 1974, 1975) and Pennycuick (1975, 1989, 1995), and derived independently by Greenewalt (1975). Total power comprises not only the aerodynamic work done by the bird, but also the heat released by the flight muscles and the energy consumed by any additional internal physiological processes. There is no physiological basis for partitioning of total energy consumed, and only minimal experimental evidence supporting values normally recommended for efficiency or postural power during flight.

Aerodynamic models: fixed wings

Birds formed the model for the technological quest for powered flight during the nineteenth and early twentieth centuries. Otto Lilienthal could not have flown the first (proven) glider without his studies of bird flight (Lilienthal, 1889), but early attempts to estimate aerodynamic forces or mechanical power during flight (e.g. De Labouret, 1889; Ahlborn, 1896; Winter, 1895) could not succeed prior to the formulation of the Prandtl–Zhukovsky–Lanchester vortex explanation of the aerofoil and the associated lifting-line model of wing action and vortex formation, in around 1910 (see, for example, Prandtl and Tietjens, 1934; von Mises, 1945). This model remains the foundation of vertebrate flight aerodynamics and leads directly to the shape of the power curve. The reasoning is straightforward.

Any wing with an aerofoil section generates a vortex wake that forces air in the wake behind the wing downwards. As a reaction to this downwards momentum, the aerofoil experiences an upwards lift force perpendicular to its motion, together with a retarding drag force. The drag has two components: the kinetic energy invested in the wake vortices gives rise to the *induced* drag, and there is also a friction and profile drag for both the wings and the body. For steady, level flight, a horizontal forward thrust must be applied to balance these drag forces.

The lift L and drag D forces are expressed in terms of lift and drag coefficients C_L and C_D, respectively, wing area S and air speed V by the familiar equations:

$$L = 0.5\rho S V^2 C_L \qquad (1)$$

and

$$D = 0.5\rho S V^2 C_D = 0.5\rho S V^2 (C_{di} + C_{D0}), \qquad (2)$$

where ρ is air density, and C_{Di} and C_{D0} represent the induced and friction components of drag, respectively. C_{D0} is approximately constant (but see below). The key prediction of lifting-line theory (e.g. Prandtl and Tietjens, 1934) is that:

$$C_{Di} \propto C_L^2. \qquad (3)$$

This is the equation of the so-called 'lift polar', and it is this that determines the shape of the power curve. In steady level flight *with a fixed wing*, lift balances weight Mg, where M is mass and $\boldsymbol{g}$ is the acceleration due to gravity, and the thrust T applied must equal the drag D. The mechanical power output P_{mech} is then given by:

$$P_{mech} = TV = DV = \frac{\alpha}{V} + \beta V^3, \qquad (4)$$

where α and β are constants that depend on the design of the aircraft of bird, on air density ρ and on $\boldsymbol{g}$, and which are generally taken to be independent of speed. The first component, the induced power, falls with speed; the second component, which combines the *profile* drag of the wings and the *parasite* drag of the body, rises with speed cubed. Therefore, the $P_{mech}(V)$ curve is necessarily U-shaped. This model takes into account only the drag forces acting on the machine and omits the additional energetic cost of generating thrust, which in aircraft is assumed to be obtained by essentially separate engines. It is at this point that the analogy between aircraft and flying animals breaks down: animals have

access to only a single source of aerodynamic force and must flap their wings so that mean aerofoil lift contributes *both* weight support and thrust. However, as I shall demonstrate below, the incremental aerodynamic cost associated with flapping wings and generating thrust is relatively small.

The first attempts to estimate the performance for flying animals applied lifting-line theory directly (e.g. Fullerton, 1911; Wieselsberger, 1914), and the earliest power curves for flying birds that I know of were computed in this way (Gnosspelius, 1925; Boel, 1929).

The most widely used model predicting animal flight performance, that of Pennycuick (1968, 1969) (see also Pennycuick, 1975, 1989; Tucker, 1973, 1974, 1975), remains founded on fixed-wing lifting-line theory. Pennycuick formulates the lifting component of his model in terms of a steady actuator disk and momentum jet (taken from propeller and helicopter theory), and the earlier forms of this model consider only the weight-supporting component of induced power. Visualization of bird and bat wake vortex structures (e.g. Magnan et al., 1938; Spedding et al., 1984; Rayner et al., 1986; Spedding, 1986, 1987b; Rayner, 1991, 1995a; Rayner and Swaddle, 1999) has shown that flapping wings do not generate a momentum jet or any structure analogous to it. Although this model is presented in terms of the actuator disk, it should properly be described as a 'lifting-line' theory since for a fixed wing the two mathematical models give algebraically identical predictions (Prandtl and Tietjens, 1934), and the lifting line is a more realistic description of the physics of wing force generation.
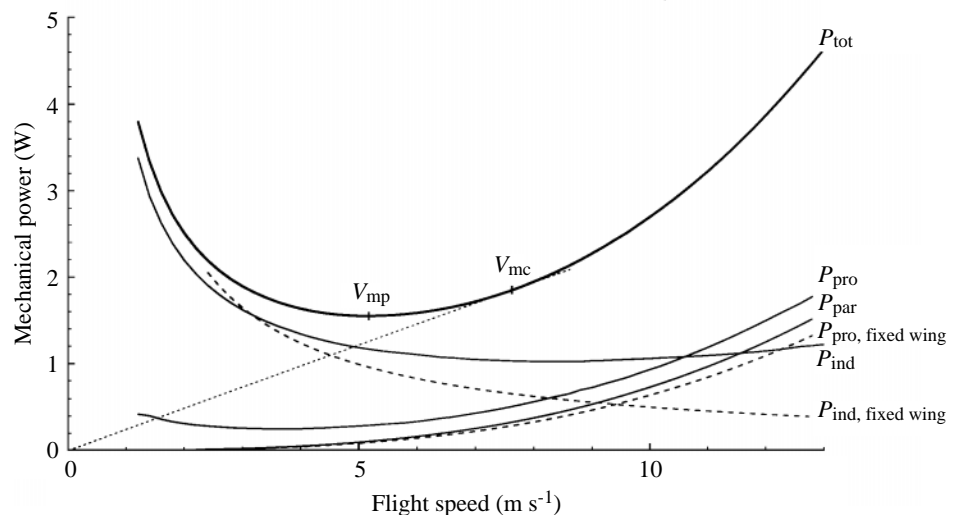
Aerodynamic models: flapping wings

There is ample experimental evidence that during fixed-wing (i.e. gliding) flight, bird and bat wings function as aerofoils (e.g. Withers, 1981; Spedding, 1987a), and therefore lifting-line aerofoil theory is an appropriate starting point for modelling animal flight. As set out above, it makes no direct prediction about the consequences of thrust from the flapping wings. The first applications of aerofoil theory to flapping flight (Fullerton, 1925; Walker, 1925, 1927) used what is now known as blade-element theory. This uses equations 1 and 2 to model individual wing sections as lifting aerofoils, without making assumptions about the relationship between lift and drag coefficients, and usually supposing that the coefficients are constant over time and/or on different parts of the wing. Although this approach has certain limitations when applied to birds and bats (Rayner, 1979a, 1986), the methodology of modelling the wing in segments remains the basis of most subsequent models of flapping flight (e.g. von Holst and Küchemann, 1941; Osborne, 1951; Cone, 1968; Betteridge and Archer, 1974; Archer et al., 1979; Rayner, 1979a,b, 1986, 1993; Phlips et al., 1981; Norberg, 1985; Ellington, 1991; DeLaurier, 1993), whether using lifting-line, blade-element or free-vortex theory. A promising development is the use of lifting-surface theory, in which vorticity is assumed to be distributed over the wings rather than concentrated onto a single line across the wingspan, but models of this kind (e.g. Smith et al., 1996; Vest and Katz, 1996) have concentrated on aerodynamic phenomena and have yet to be applied to predict flight performance or power curves.

Flapping bird and bat wings use the same aerodynamic mechanisms to generate wake vortices as do fixed wings, but the vortex geometry is more complex (e.g. Rayner, 1995a). Vortices do not lie in a plane behind the animal, but are distributed spatially according to the movements of the wings. This problem may be tackled by free-vortex theory (first pursued for bird flight by Cone, 1968), which extends lifting-line theory to unsteady wing movements. In steady forward flight, birds and bats choose from two gaits, which can be distinguished by the aerodynamic function of the upstroke and by wingbeat kinematics (Rayner, 1988, 1993, 2000; Spedding, 1992; see also below). I have used the free-vortex approach to develop theoretical models of aerodynamic force production and power output in the two gaits

Fig. 1. Mechanical power curves computed for a typical bird (the Eurasian kestrel *Falco tinnunculus*) using the continuous vortex model of Rayner (1986, 1993). This is a fully unsteady implementation of lifting-line theory, incorporating realistic descriptions of wingbeat kinematics and wake structure (derived from flow visualization experiments by Spedding, 1987b). Heavy continuous curve, total mechanical power P_{tot}; thin continuous curves, induced P_{ind}, profile P_{pro} and parasite P_{par} components of aerodynamic power; dashed curves show, for comparison, the profile and induced power components for an equivalent fixed-wing aircraft of the same design: the differences between these lines and the corresponding continuous curve show the cost of generating thrust by flapping the wings (taken from Rayner, 1995b, with permission). V_{mp} and V_{mc} are, respectively, the speeds that minimize mechanical power and cost of transport (energy per unit distance); the latter is defined as the point where a tangent from the origin (dotted line) meets the curve.

(Rayner, 1979a,b, 1986, 1993). These models permit explicit quantification of the enhanced cost of generating thrust (Fig. 1). Induced power does not decline as the inverse of speed, but rises slightly at the highest speeds: this is to be expected since more air must be accelerated backwards to provide the necessary thrust to balance high friction drag. In addition, profile power must increase because the wing sections travel faster during flapping. The result of these two effects is that the mechanical power curve has a slightly shallower minimum than predicted by equation 4. Of the order of 25 % of the mechanical work done during flapping is associated with generating thrust.

Aerodynamic models of flapping flight appear to describe correctly the physical processes involved in the generation of aerodynamic force. Induced power is likely to be the most realistic and has been shown by Spedding (1987b) and Rayner (1993) to coincide well with direct measurements in flow visualization experiments. The major problem with models of this kind lies in estimation of appropriate values for drag coefficients, which are not well known for birds or bats. Pennycuick (1969) proposed that profile power, which is the rate of working against lift-independent wing drag, should be modelled as being independent of speed in flying birds; effectively, the profile drag coefficient decreases sharply with speed; this is the most distinctive component of his model, but is based on a number of assumptions that have not been tested (Rayner and Ward, 1999). No other model of flight performance has accepted this model of profile power; all others have followed the aircraft analogy and allowed profile power to increase as speed cubed. Profile power remains the least understood of the components of aerodynamic power in flight. Until reliable measurements of profile drag coefficient for a range of bird wings become available and the effect of flapping on those coefficients is thoroughly understood, the optimum strategy must be to assume that the coefficient is constant and to use values measured from real bird wings.

Parasite power is also modelled as increasing as the cube of speed; drag coefficients are normally estimated from scaling formulae extrapolated from measurements on a small number of frozen bird bodies (e.g. Tucker, 1973), mainly from relatively large species. Recently, Pennycuick et al. (1996) have argued that, if Pennycuick's (1989) model is to predict metabolic power (see below) and flight behaviour accurately, then body drag estimates must be reduced by a factor of as much as eight (the possibility that profile power or flight muscle efficiency is wrongly estimated was not considered). Measurements in my own laboratory (W. J. Maybury and J. M. V. Rayner, unpublished results) indicate that body drag coefficients in passerine and other relatively small birds are of the order of one-third or half of those derived from the normal formulae and that parasite drag coefficients tend to decrease with air speed. If this result is confirmed and shown to be typical of birds, then existing aerodynamic models overestimate power significantly, and these findings may have significant implications for the interpretation of bird flight performance.

Metabolic power

As explained above, according to the model of Pennycuick and Tucker, total or *metabolic* power P_{met} can be derived from aerodynamic power by the method outlined above, which may be expressed as the equation:

$$P_{met} = \frac{k_{pos}}{\eta} P_{mech} + P_{b}, \quad (5)$$

where P_{b} is basal metabolic rate, k_{pos} is a factor representing the 'postural' cost of flight and η is the flight muscle efficiency. P_{met} is an estimate of the total rate of energy output by the animal in flight; in steady conditions, it should be equal to the mean rate of energy input, which may be determined by the oxygen uptake to metabolize fuel. If P_{b}, k_{pos} and η are independent of speed (and this is probably unlikely), then the metabolic power curve will have the same U-shaped profile as the mechanical power curve. Tucker (1973) and Pennycuick (1975, 1989) proposed a constant value of 23–25 % for η, and modelled postural power as a multiple of mechanical power ($k_{pos} \approx 1.1$). There is no direct experimental evidence for either supposition. The mechanical component P_{mech} can be defined rigorously as the energy used to perform aerodynamic work in flight; the additional – and much larger – component released as heat by a range of processes is poorly understood. It is unjustified to assume that basal metabolic rate, 'postural' power (as far as such a quantity exists) and energy released as heat are independent. For example, there is an important mechanical linkage between thoracic muscle activity and respiration (Jenkins et al., 1988); driving this mechanism may represent an additional mechanical energy cost, but it may be powered by the flapping wings and deforming thorax.

The most serious limitation with this approach is that there is insufficient independent evidence for the suggested values of flight muscle efficiency. Flight in tilting wind tunnels cannot be used to estimate it since this method fails to take account of the differential costs of thrust generation at different flight angles (Rayner, 1986), but has tended to indicate efficiencies of the order of 20–30 % (e.g. Tucker, 1972). The *whole-animal efficiency* introduced by Ward et al. (1999b) circumvents some of these limitations. This quantity has no direct physiological basis other than to summarize all components of energy released by the bird not attributable directly to flight mechanics; it is a convenient way of expressing the relationship between the (known) mechanical power and the much larger metabolic power consumed. Comparison of measured metabolic and computed mechanical powers (Rayner, 1995b) suggests that whole-animal efficiency increases sharply with size (approximately as body mass to the power 0.25) and may be 10 % or less in the smallest birds. Values of 10 % have been estimated for hovering hummingbirds (Chai and Dudley, 1995). If postural and basal metabolic powers are as proposed by Pennycuick (1989), then muscle efficiency for most birds is much smaller than 25 % and reaches this value only in the largest flapping birds. Our direct estimates in starlings (below) give whole-animal efficiency in the range 12–18 %, and estimated flight muscle efficiency

below 20 % (Ward et al., 1999a). Estimating total power by extrapolation from aerodynamic power will inevitably be inaccurate: these values of efficiency mean that total power is 4–10 times larger than the aerodynamic component; however well the aerodynamic energy is known, inaccuracies in total power are unavoidable.

An alternative approach is provided by a recent analysis modelling the physiological processes in hearts, lungs and flight muscle mitochondria; this explains the observed scaling of metabolic power output and efficiency with body size across the size range of birds (Bishop, 1997; Bishop and Butler, 1995), but does not yet have the resolution to predict variation in efficiency with speed.

One approach to determining unknown parameters such as C_{D0}, k_{pos} and η, which was adopted by Tucker (1973) and Greenewalt (1975) in formulating their models and has been advocated by Pennycuick (1989), is to estimate such quantities by fitting to available direct measurements of energy uptake. The resulting formulae might give good estimates for flight performance of some animals in some conditions, but any subsequent tests of model predictions are circular; there is no insight into the underlying functional parameters, and the models cannot be abstracted to other species with any confidence. This strategy cannot be recommended. It is greatly preferable to quantify the extent of uncertainty in model predictions arising from uncertainty in parameter values and to

use this as a basis for focusing attention on the quantities or assumptions to which the predictions are most sensitive.

With the present level of confidence in the models, estimation of the maximum range and minimum power speeds that characterize the power curves (Pennycuick, 1969; Rayner, 1985a, 1990; Hedenström and Alerstam, 1995) is relatively unreliable, since the minima of both mechanical and metabolic power curves are rather shallow, and the curves are sensitive to the poorly known drag values. Welham (1994) has shown that models do not predict flight speeds well, and Rayner (1994b) has established a systematic bias in estimation of characteristic powers that can be explained by the size-dependence of whole-animal efficiency.

Direct measurement of power output

Metabolic power

The alternative to theoretical modelling is to measure power output directly. Each of the three main techniques employed for determining total power (mass loss, gas exchange, labelled isotopes; see, for example, Masman and Klaasen, 1987; Rayner, 1990) has now been used to measure power curves for birds and bats flying in wind tunnels (Fig. 2). Possible limitations of these methods were reviewed by Rayner (1994a) and Rayner and Ward (1999) but, these concerns apart, these measurements provide the best available insight into energy consumption in flight.

Fig. 2. Metabolic power curves measured for birds and bats flying in wind tunnels, shown (A) as absolute measurements and (B) normalized relative to predicted performance at minimum power flight speed. This scaling is an approximate method of eliminating the effects of size. Taken from Rayner, 1994a, with permission, where full details of sources were given; these figures do not include more recent measurements by Kvist et al. (1998) and those of Ward et al. (1999a,b) summarized in this review.
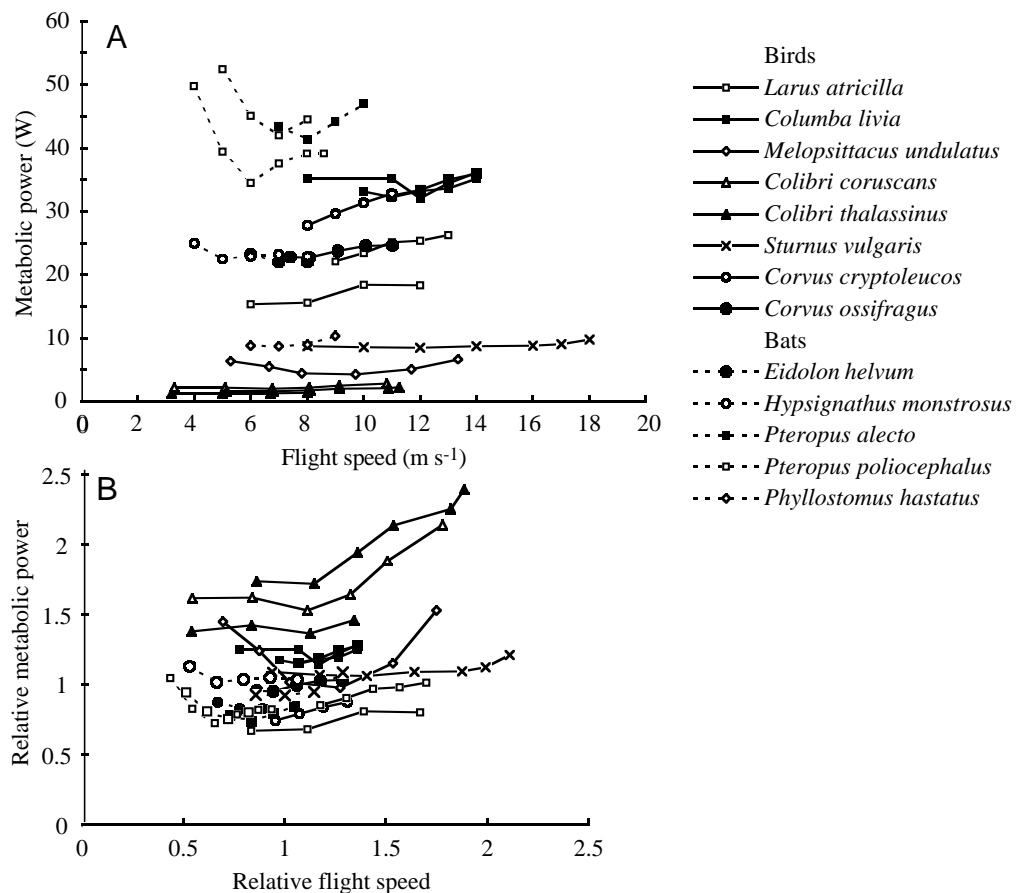
Fig. 3. Validation of mechanical power models by direct measurements and wingbeat kinematics. (A) Total mechanical power P_{tot} (+) and induced P_{ind}, profile P_{pro} and parasite P_{par} components of aerodynamic power output plotted against speed for a magpie *Pica pica* computed using the vortex-ring model of Rayner (1979a), using kinematics from Tobalske and Dial (1996). This estimated aerodynamic power is compared with direct measurements of mechanical power delivered at the shoulder joint from Dial et al. (1997) (×). The agreement between predicted aerodynamic power and measured power at the shoulder is good. Wingtip tracings reveal that magpies use the vortex ring gait during steady and accelerating flight, but the continuous vortex gait when decelerating (Tobalske and Dial, 1996). (B) Mechanical power curves for a pigeon *Columba livia* computed using (open circles) vortex-ring (VR) (Rayner, 1979a) and (open squares) continuous-vortex (CV) models (Rayner, 1986, 1993), with kinematics from Tobalske and Dial (1996). From observation and measured kinematics, the bird changes gait at $12–14\,\mathrm{m\,s^{-1}}$ (Tobalske and Dial, 1996), which is the speed range where the two mechanical power curves coincide; below this speed, the continuous vortex gait is more expensive because of the high upstroke drag and the cost of the excess downstroke thrust.
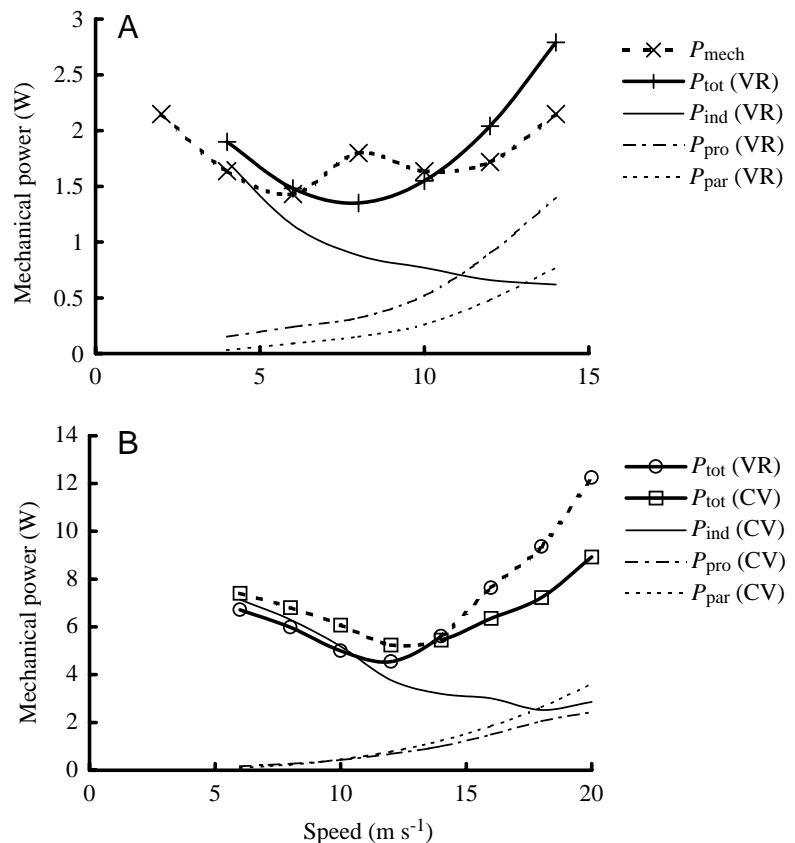
Aerodynamic power output

In principle, it should be possible to obtain an estimate of P_{mech} by sampling the wake of a flying bird. So far, this has been achieved only in birds flying in still air at uncontrolled speeds (for a review, see Rayner, 1995a), but similar methods should work in a wind tunnel provided that the airflow is of high quality.

An alternative method that has met some success is to measure force from the flight muscles by implanting miniature strain gauges on the delto-pectoral crest of the humerus; this has been used to obtain mechanical power/speed curves for a magpie *Pica pica* (Dial et al., 1997). Predictions of aerodynamic power from free-vortex theory agree remarkably well with initial results with this technique (J. M. V. Rayner, in preparation; Fig. 3A). At higher speeds, mechanical power is slightly lower than predicted, and there are several possible explanations for this discrepancy: (1) the aerodynamic model overestimates power, probably through overestimating drag; (2) the strain gauge measures displacement of the humeral crest, but not rotation of the humerus (*sensu* Poore et al., 1997), which provides a major component of wingtip movement and therefore of aerodynamic force generation; (3) the assumption that the geometric strain in pectoralis fibres is proportional to wingbeat amplitude may be false. In future, it is likely that these limitations will be resolved, and this will represent a powerful method which can be validated alongside measurement of aerodynamic power output. This comparison of measurement and prediction represents the first occasion on which predictions of an aerodynamic power model have been validated against direct measurement.

The shape(s) of power curves

Considerable debate has surrounded the shape of measured metabolic power curves, which rarely conform to the smooth U-shaped profile predicted by aerodynamic models. This has led to discussion about whether power curves are properly U-, J- or L-shaped: for J-shaped curves, power during hovering or slow flight is not high, while for L-shaped curves power does not rise as speed increases (Ellington, 1991; Alexander, 1997). The collated published measurements (Fig. 2) reveal some of the difficulties, particularly when shown in size-corrected form. For some species, for example the budgerigar *Melopsittacus undulatus*, the curves are clearly U-shaped, as they are for recent measurements on several species using the mass-loss technique (Kvist et al., 1998). For other species, they are flatter than expected. For most species, a minimum power can be identified, and power rises as expected at higher speeds. Few measurements have been obtained of power during slow forward flight, and birds are often reluctant to fly slowly in wind tunnels. The starling *Sturnus vulgaris* in the measurements of Torre-Bueno and Larochelle (1978) is exceptional in that there is only a marginal increase in power up to the highest speeds. This measurement has been used to argue both that power is independent of speed and that the power curve is L-shaped. More recent experiments with this

species (see below and Fig. 4) have found a more normal increase in power with speed; the older measurements may be discounted, and the abnormal results are perhaps due to the design of the wind tunnel used (S. Vogel, personal communication). Dial et al. (1997) used their measurements of mechanical power at the shoulder joint to propose further evidence for an L-shaped relationship, but the interpretation is largely a matter of perception; the curves do not differ from a predicted U shape (Fig. 3A), and the L shape for mechanical or aerodynamic power is inconsistent with the known rise in drag at high speeds.

A number of possible explanations have been advanced for the differences in the shape of the power curve between the animals studied, and between the measured curves and the expected U shape. Ellington (1991) has argued that curves should be J-shaped because, in hummingbirds *Colibri* spp., minimum power is close to that measured during hovering, in the same species, by the same author (Berger, 1985). One interpretation is that these hummingbird forward flight measurements were made in an open-section wind tunnel, which will increase mechanical power compared with free flight (Rayner, 1994a). However, recent measurements of metabolic power in hovering glossophagine bats (Voigt and Winter, 1999) have shown that metabolic power scales differently with size in hovering and in forward flight. Thus, the mechanical power/speed curve is always U-shaped, but in smaller animals the metabolic curve is J-shaped, but would become more U-shaped as size increases. Insect power curves may be J-shaped because of this differential scaling or because of the impact of unsteady aerodynamic lifting mechanisms (see Ellington, 1991).

In reality these U-, J- and L-shaped hypotheses should not be viewed as alternatives but as elements of a continuum. To demonstrate this, I propose three assumptions. First, that the mechanical power curve is U-shaped: it is inescapable that drag will increase at the highest speeds, and all aerodynamic models concur that induced power is high at low speeds. Second, that metabolic power is close to a linear function of mechanical power, as in equation 5; this assumption is less robust. Third, that a flying animal will do as much as possible to minimize flight power, and that evolution will have optimized power consumption in flapping flight as far as feasible (this is an issue I return to below). Then, the shape of an empirical metabolic power curve will be similar to the mechanical curve, and perception of that shape will depend on the range of speeds over which it is measured; this range will probably encompass the *minimum power speed* which defines the 'bottom' of the U, and may not include those speeds at which power is predicted to be high simply because animals are reluctant to invest large amounts of energy. The minimum is likely to be hard to determine with any accuracy from empirical measurements, particularly in view of experimental error and natural variation. Predicted curves are shallow about the minimum, and a measured curve may be equally amenable to description as flat or as U-, J- or L-shaped.

Hypotheses about curve shape should not be explored simply by the appearance of the curve, but should be tested by comparison of measurements with a formal theoretical prediction; however, there have been few attempts to test shape statistically. The hypothesis that power is independent of speed (i.e. that the power curve is flat) is inappropriate since it has no basis in the physics of flight; moreover, a simple linear regression test of power against speed can be misleading since it cannot distinguish a horizontal line ($P=0$) from a segment of a U- (or J- or L-) shaped curve; the only case when regression can be useful is when it is used to test for an increase in power with speed towards the upper speed range, which may confirm a segment of a U-shaped relationship. A preferable null hypothesis is that the curve does not differ from a predicted U-shape predicted by equations 4 and 5 or equivalent models. It is not sufficient to find a significant fit to a generalized metabolic power curve:

$$P = \frac{\alpha'}{V} + \beta'V^3 + \gamma \qquad (6)$$

derived from equations 4 and 5 with arbitrary parameters α', β' or γ, since confidence limits for estimation of these parameters will in most cases be very broad, and the values of these parameters could be meaningless. The only viable statistical test of power curve shape is to compare (by analysis of covariance) the accuracy of the fit between measured and estimated powers; however, this test has little statistical power and in the absence of robust physiological modelling it is more valuable to use available experimental measurements to estimate parameters such as efficiency. If such tests are performed for the experimental data in Fig. 2B using Pennycuick's (1989) model, none of the fits fails to reach significance (J. M. V. Rayner, unpublished results; see also Kvist et al., 1998).

Although the first and third of the assumptions I made above are robust, the second, that efficiency and 'internal' metabolic power components are independent of speed, is not. A realistic explanation for differences in shape between metabolic and mechanical power curves lies in current limited quantitative knowledge of internal physiological processes. I have argued (Rayner, 1979b) that flight muscle efficiency should be dependent on flight speed, since wingbeat kinematics, and therefore muscle contraction dynamics, must vary to control thrust. Speed-related variations in efficiency will mean that metabolic and mechanical power curves may not coincide in shape. Optimum flight speeds (*sensu* Hedenström and Alerstam, 1995) cannot usefully be predicted from mechanical power, or from metabolic power estimated with constant efficiency. By tuning muscle kinetics to preferred flight patterns, animals may have access to adaptive mechanisms of optimizing flight performance independent of flight behaviour, and there are some indications that birds vary such parameters seasonally in response to life history dynamics and critical periods such as moult (Rayner and Swaddle, 1999) and migration. This process could potentially produce substantial differences in

metabolic power curve shapes among species which the available measurements have as yet been insufficient to distinguish.

Integrated approach to starling flight energetics

To determine possible variation in efficiency with speed, a recent collaborative study (Ward et al., 1999a,b; Rayner and Ward, 1999) has measured components of flight power in European starlings *Sturnus vulgaris* using a range of methods applied to the same group of animals, both in the field in Scotland and in a wind tunnel at the Universität des Saarlandes at Saarbrücken in Germany. The starling is an appropriate model species since it is often studied in behavioural and field ecology, and its life history is well understood. One goal of the study was to repeat the measurements of Torre-Bueno and Larochelle (1978) which, as explained above, appear anomalous. Full details of this work will be published elsewhere (Ward et al., 1999a,b; S. Ward, J. R. Speakman, J. M. V. Rayner, U. Möller, D. M. Jackson and W. Nachtigall, in preparation); a brief summary of our results for starling power curves is given here.

The most important finding is that measurements of total metabolic power output over a range of flight speeds by both oxygen uptake through a respiratory mask (Fig. 4A) and labelled isotope methods give similar values and show a statistically significant increase with speed ($F_{1,19}=24.3$ for bird 1, $F_{1,22}=102.5$ for bird 2); only the portion of the power curve around and above the minimum power speed of approximately $7\,\mathrm{m\,s^{-1}}$ was measured. These experiments are the first to have used the labelled isotope technique to assay metabolic rate at varying speed in a wind tunnel and to have validated this technique simultaneously with direct measurement of gas exchange in an active flying bird; they successfully confirm that this less-invasive technique is viable for birds provided that flight times of 1 h or greater can be achieved. The wind tunnel measurements are also congruent with labelled isotope measurements in the field (S. Ward, J. R. Speakman, J. M. V. Rayner, U. Möller, D. M. Jackson and W. Nachtigall, unpublished results; approximately 9 W, Westerterp and Drent, 1984). Our birds exploited tunnel boundary effects by flying near the upper surface and, at higher speeds, used flap-gliding or undulating flight (Rayner, 1985b) extensively to reduce mechanical power, possibly to compensate for increased energy costs associated with flight inside the tunnel. Our measured power in the wind tunnel markedly exceeds the values previously published by Torre-Bueno and Larochelle (1978), especially at higher speed; we are confident that the earlier measurements are not realistic and that starlings do not have a 'flat' power curve.

The increase in metabolic power with speed is much less steep than that of mechanical power, which we estimated using Pennycuick's (1989) model with default parameters and using Rayner's (1979a) vortex-ring model (Rayner and Ward, 1999) with wingbeat kinematics measured by U. Möller (unpublished results; see also Ward et al., 1999b). Estimates from the two models did not differ significantly from one another, but can be reconciled with the metabolic power measurements only if whole-animal efficiency is very much lower than anticipated and increases with flight speed (Fig. 4B). It lies in the range 12–15 % at lower flight speeds and increases significantly to 17–20 % at higher speeds. If basal and postural metabolic rate are estimated following Pennycuick (1989) and equation 5, then flight muscle efficiency exceeds 20 % only at the highest speeds. This means that, if our estimates of aerodynamic or mechanical power are accurate, at most one-fifth, and at low speeds as little as one-eighth, of the energy leaving the bird is
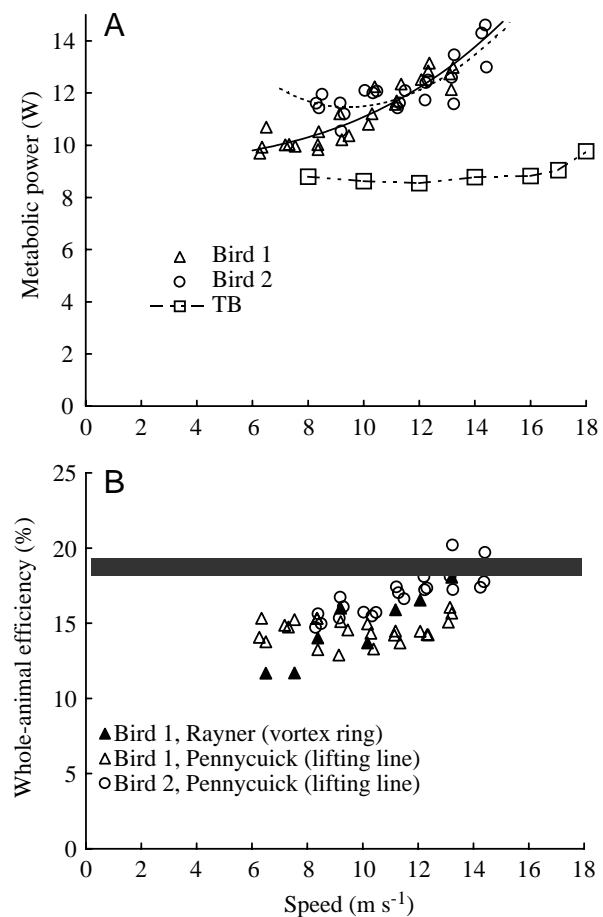

Fig. 4. Starling power curves and whole-animal efficiency (S. Ward, U. Möller, J. M. V. Rayner, D. M. Jackson, D. Bilo, W. Nachtigall and J. R. Speakman, in preparation). (A) Metabolic power for European starlings measured by gas exchange for two individual birds by S. Ward, U. Möller, J. M. V. Rayner, D. M. Jackson, D. Bilo, W. Nachtigall and J. R. Speakman (unpublished results) at Universität des Saarlandes during 1996–1998, with a respiratory mask (curves fitted using equation 6), and measured for slightly lighter birds by Torre-Bueno and Larochelle (1978) (TBL). (B) Whole-animal efficiency during flight determined using mechanical power computed for two European starlings using two alternative aerodynamic methods (models of Rayner and Pennycuick; see text), allowing for variation in air density and for the drag and weight of the respiratory mask and for Rayner's vortex-ring model with measured wingbeat kinematics. The shaded bar shows the likely whole-animal efficiency with flight muscle efficiency equal to 23 %.

useful aerodynamic work. The remainder is released as heat. The relative magnitudes of aerodynamic and thermal powers may vary among species, most notably in response to size (Rayner, 1995b).

To confirm this estimate of efficiency in starlings, we developed simultaneously the method of digital video thermography to quantify the heat released by the bird (Ward et al., 1999b). This proved particularly effective. While further analytical development is needed to refine estimates of heat transfer by aerodynamic convection, initial results show that thermal power is between 80 and 90 % of measured metabolic power (see above) and is close to the difference between measured metabolic and estimated mechanical power. This finding gives us considerable confidence that all the methods we employed are reliable and validates both sets of direct metabolic power measurements; it provides an additional, and more accurate, measure of the whole-animal efficiency. The non-invasive thermography technique has considerable promise as a means of estimating flight energy for both captive and free-flying birds.

I discussed above how the commonly used estimates of body parasite drag may be too high. As a result, the estimated mechanical power used here may also be slightly too high. If the estimate of parasite drag is reduced by 50 %, then whole-animal efficiency would be depressed still further below the 23–25 % range, and in starlings would fall in the range 9–16 %. An alternative explanation of the apparent increase in whole-animal efficiency with speed is that parasite power does not increase as steeply as speed cubed, and so mechanical power is overestimated at high speeds. If it is assumed that whole-animal efficiency is constant and is correctly estimated at around the apparent minimum power speed, then the measured metabolic rates during flight can be explained only if parasite (or profile) drag coefficients are overestimated at high speeds by as much as 30 %. Available measurements and estimates of drag are not consistent with such a large discrepancy.

Discussion

Power curves and gaits

The aerodynamic power required for an animal to fly must follow a U-shaped curve. Induced power required for hovering or very slow flight is greater than for forward flight because of the greater volume of air that must be accelerated by the flapping wings. Parasite and profile powers must increase during fast forward flight because of the increasing frictional drag. A bird may manipulate its power curve by changing its flight behaviour or by controlling its morphology, but the physical constraints of weight and drag cannot be circumvented and, as demonstrated by the lifting-line model described above, it is these that determine the shape of the power curves.

Physiological processes in the conversion of fuel to aerodynamic work are indirectly dependent on speed, and the total power curve may have a very different shape. In the experiments on starlings reported above, we found that efficiency increases with speed so that the increase in the metabolic power curve is less steep. There is no reason to suppose that the same should happen in every bird species.

The major challenge is now to understand in more detail the physiological processes that mediate the performance of aerodynamic work. A bird will make behavioural decisions about foraging and flying on the basis of the *metabolic* power curve, and it is likely that certain behavioural strategies during flight themselves determine the power curves. I identify three separate mechanisms by which this might occur. First, as mentioned above, flight in ground effect and intermittent-flight strategies modify the mean rate of performing aerodynamic work. Second, a bird must control its wingbeat kinematics (e.g. frequency, amplitude, upstroke flexure, etc.) to fly at different speeds. This is one of the mechanisms by which a bird gears the power output of the flight muscles to the aerodynamic power required. Stress, strain and strain rate in the flight muscles all change with speed, and a bird is therefore likely to experience varying flight muscle efficiency. The starling experiments indicate that the range of variation in efficiency with speed (10–20 %) is considerable. Third, birds may be unable to vary their kinematics – and therefore thrust and power output – enough over a range of speeds to optimize mechanical work output; instead, they change gait by changing the aerodynamic function of the upstroke at a characteristic speed (Rayner, 1986, 1995a; Tobalske and Dial, 1996; Alexander, 1989, 1997). The kinematic and morphological features of the two gaits used by birds and bats in steady forward flight are reviewed elsewhere (Rayner, 1988, 2000).

In an analogous situation, terrestrial mammals do not have a single smooth power curve, but there are three separate U-shaped curves of metabolic energy per unit distance corresponding to the three gaits, walk, trot and canter (Hoyt and Taylor, 1981). Power consumption is one of the factors implicated in gait selection by running mammals, but gait transitions are triggered by stresses in leg bones and muscles (Farley and Taylor, 1991). It is possible that something similar happens in birds and bats as they change gait. Preliminary estimates (Fig. 3B) of mechanical power in flying pigeons based on free-vortex models, flow visualization experiments (Spedding et al., 1984) and wingbeat kinematics measured in a wind tunnel by Tobalske and Dial (1996) suggest that the aerodynamic power curves for the two gaits are distinct and that they intersect at the same speed range because a sharp difference can be distinguished in upstroke function from wingtip tracings (Tobalske and Dial, 1996). As yet, measured power curves for pigeons or other species do not have the sensitivity to show this effect in metabolic power consumption. In birds and bats (Rayner et al., 1986; Rayner, 1995a), gait transitions in accelerating flight are rapid and are expected to occur when the cost in induced drag of generating lift on the upstroke exceeds the benefit of supporting the weight (Rayner, 1993).

The power curve and constraints on flight performance

The principles that birds adjust their wingbeat kinematics or

flight behaviour to control speed and that flight muscle efficiency varies concomitantly lead to a further hypothesis that may be of considerable significance for the interpretation of behavioural strategies during flight. We cannot be certain that the whole range of speeds is available to every species of flying animal. Some speeds may correspond to kinematic patterns that are inconsistent with the anatomy of the wings and pectoral girdle, which cannot generate sufficient lift or thrust, or which correspond to excessively low flight muscle efficiencies or unacceptably high mechanical power (possibly, for instance, at speeds where the curves intersect in Fig. 3B). Mechanisms of this kind could be expected to be responsible for constraints on flight speed and are implicated in gait changes. The consequence of them is that a bird's perception of the power/speed curve may differ substantially from the smooth curves that are the currency of theoretical models. In the extreme – and hypothetical – case, the power curve may simply not exist, but mechanical, physiological and autotrophic (such as sensory perception or prey behaviour) factors constrain a bird to a narrow choice of flight speeds for which its flight system is well adapted and which are consistent with its life history and its use of its environment. Although it seems optimal for evolution to select bird designs that are flexible and are not constrained in this way, it is possible to envisage circumstances in which a species has become adapted for highly specialized and mechanically stereotyped behaviours. Presumably, this is not the case for animals that have demonstrated the ability to fly comfortably at a wide range of speeds in a wind tunnel. However, the hypothesis that this is not the case for *all* species has not formally been tested. Further

exploration of this hypothesis needs a better understanding of the potential for mechanical and physiological properties of the flight muscles and for wingbeat kinematic patterns to impose constraints on the evolution and radiation of the flight system and on flight speed selection.

Experimental tests for the existence of constraints of this kind are often impractical, since as an animal approaches a constraint its perceives an increased risk of injury, a reduction in safety factor or a diminution of performance. However, two factors related to constraints of this kind can be explored. Pennycuick (1969) showed how the accessible range of flight speeds can be constrained by a limit on mechanical power output. There is some debate about appropriate values for maximum power and about how it depends on muscle size, contraction frequency and other factors. It is known that the mechanical power available from bird muscles increases with size much less rapidly than the aerodynamic power required to fly: as a result, larger birds cannot hover or fly very fast, and larger species are constrained in take-off ability (Pennycuick, 1969, 1975; Rayner, 1995b, 1996). Pennycuick (1969) proposed that the maximum mechanical power for any individual is independent of speed; this may not be realistic since the maximum power that may be delivered depends on muscle kinetics and, therefore, on wingbeat kinematics. It is also unknown whether the most rigorous constraint is imposed by mechanical power output or – in steady flight – by delivery of oxygen to the flight muscles or by other physiological factors.

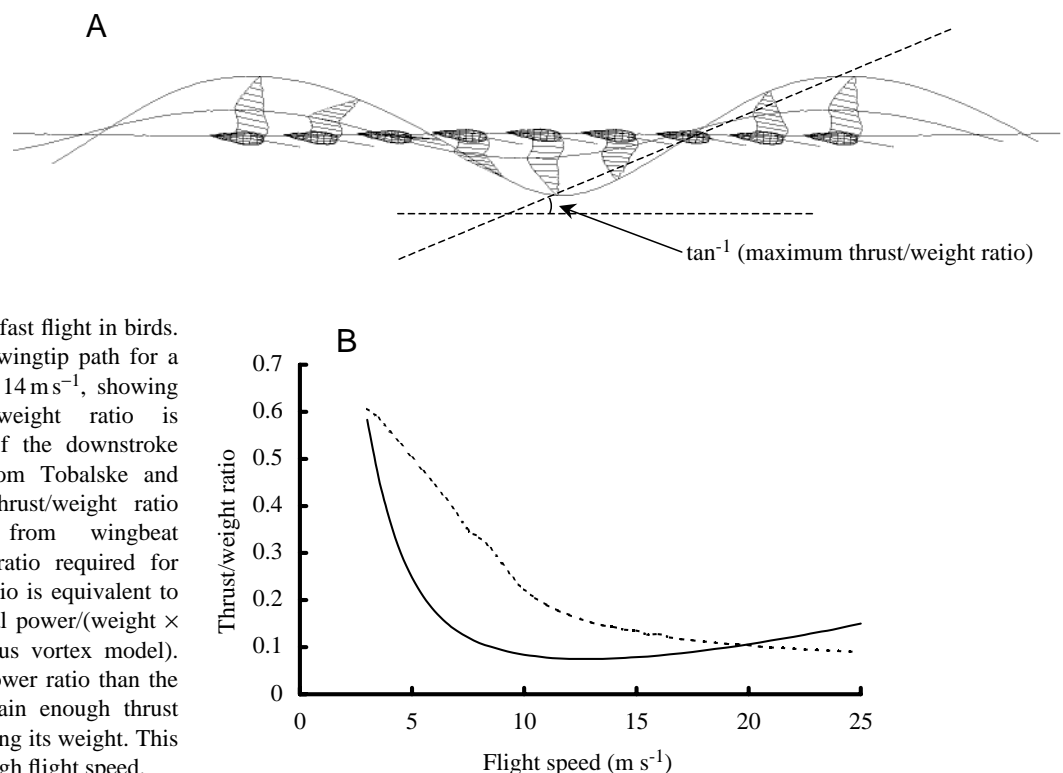An important constraint is also imposed by wingbeat kinematics and the balance of aerodynamic forces on the

Fig. 5. Kinematic constraints on fast flight in birds. (A) Diagrammatic view of the wingtip path for a pigeon *Columba livia* flying at $14\,\mathrm{m\,s^{-1}}$, showing how the maximum thrust/weight ratio is determined by the geometry of the downstroke (frequency, amplitude, etc., from Tobalske and Dial, 1996). (B) Maximum thrust/weight ratio (dashed line) determined from wingbeat kinematics, and thrust/weight ratio required for steady flight (solid line); this ratio is equivalent to the cost of transport [mechanical power/(weight × speed)] from Fig. 3B (continuous vortex model). When the dashed line gives a lower ratio than the solid line, the bird cannot obtain enough thrust during level flight while supporting its weight. This forms a probable constraint on high flight speed.

animal. This can be visualized geometrically (Fig. 5). The lift generated by the wings must both support the weight and provide the thrust that balances the parasite drag on the body and the induced and profile drags on the wings. The maximum ratio between thrust and weight is determined by the path of the wingtip relative to the air (Fig. 5A); as speed increases, the ratio corresponding to the downstroke angle becomes shallower (Fig. 5B, dashed line). The required thrust is determined by the drag, and the required thrust/weight ratio is identical to the cost of transport [mechanical power/(weight × speed)]. The cost of transport falls to a shallow minimum and then increases (Fig. 5B, solid curve). There is therefore a critical speed above which a bird cannot sustain steady level flight, because there would either be insufficient thrust or excess vertical force. Evidence that birds do experience this constraint comes from changes in wingbeat kinematics as speed increases: the stroke plane in the downstroke becomes anterio-posteriorly slanted, and the relative duration of the downstroke falls (Tobalske and Dial, 1996) so that the downstroke angle is maintained as large as possible. (The maximum speed at which a pigeon would fly in a wind tunnel was $20\,\mathrm{m\,s^{-1}}$, which coincides well with the estimated maximum.) The critical speed appears to be very sensitive to body size and wing morphology, and may also be sensitive to flight environment, for instance in a wind tunnel. It appears to be relatively low in short-winged and smaller birds. I suggest that it is this constraint, rather than a limit to available power, that determines maximum flight speed in many flying animals.

In addition to modifying wingbeat kinematics, there are two possible responses to this situation. One may be to adopt an alternative gait with a different relationship between thrust and lift; this is the situation in which a hypothetical 'third' flapping gait is most likely to be adopted; flow visualization experiments have not yet been performed at sufficiently high speeds. The other, which is most appropriate for small birds that can power the accelerations required, is to adopt some form of intermittent flight, in which the excess vertical force at the highest flight speeds is translated into height gain. This hypothesis, to be tested in the future, might mean that smaller birds are simply unable to fly level and steadily.

References

Ahlborn, F. (1896). Zur Mechanik des Vogelfluges. *Abh. Naturw. Ver. Hamburg* **14**, 1–134.

Alexander, R. McN. (1989). Optimization and gaits in the locomotion of vertebrates. *Physiol. Rev.* **69**, 1199–1227.

Alexander, R. McN. (1997). The U, J and L of bird flight. *Nature* **390**, 13.

Archer, R. D., Sapuppo, J. and Betteridge, D. S. (1979). Propulsion characteristics of flapping wings. *Aero. J.* **83**, 355–371.

Berger, M. (1985). Sauerstoffverbrauch von Kolibris (*Colibri coruscans* und *C. thalassinus*) beim Horizontalflug. In *Biona Report 3, Bird Flight – Vogelflug* (ed. W. Nachtigall), pp. 307–314. Stuttgart: Gustav Fischer.

Betteridge, D. S. and Archer, R. D. (1974). A study of the mechanics of flapping wings. *Aero. Q.* **25**, 129–142.

Bishop, C. M. (1997). Heart mass and the maximum cardiac output of birds and mammals, implications for estimating the maximum aerobic power input of flying animals. *Phil. Trans. R. Soc. Lond. B* **352**, 447–456.

Bishop, C. M. and Butler, P. J. (1995). Physiological modeling of oxygen consumption in birds during flight. *J. Exp. Biol.* **198**, 2153–2163.

Boel, M. (1929). Scientific studies of natural flight. *Trans. Am. Soc. Mech. Engrs* **51**, 217–242.

Chai, P. and Dudley, R. (1995). Limits to vertebrate locomotor energetics suggested by hummingbirds hovering in heliox. *Nature* **377**, 722–724.

Cone, C. D. (1968). The aerodynamics of flapping bird flight. *Spec. Sci. Rep. Va Inst. Mar. Sci.* **52**.

De Labouret, Ch.-M. (1889). Calcul des forces mises en jeu dans le vol des oiseaux. In *Le Vol des Oiseaux* (by E. J. Marey), pp. 339–382. Paris: G. Masson.

DeLaurier, J. D. (1993). An aerodynamic model for flapping-wing flight. *Aero. J.* **97**, 125–130.

Dial, K. P., Biewener, A. A., Tobalske, B. W. and Warrick, D. R. (1997). Mechanical power output of bird flight. *Nature* **390**, 67–70.

Ellington, C. P. (1991). Limitations on animal flight performance. *J. Exp. Biol.* **160**, 71–91.

Farley, C. T. and Taylor, C. T. (1991). A mechanical trigger for the trot–gallop transition in horses. *Science* **253**, 306–308.

Fullerton, J. D. (1911). (ed.) *First Report of the Bird Construction Committee*. London: Aeronautical Society.

Fullerton, J. D. (1925). The flight of birds. *J. R. Aero. Soc.* **29**, 535–543, 595–597.

Gnosspelius, O. F. (1925). Notes [to J. D. Fullerton 'The flight of birds']. *J. R. Aero. Soc.* **29**, 543–547, 648–649.

Greenewalt, C. H. (1975). The flight of birds. *Trans. Am. Phil. Soc.* **65**, part 4.

Hedenström, A. and Alerstam, T. (1995). Optimal flight speed of birds. *Phil. Trans. R. Soc. Lond. B* **348**, 471–487.

Houston, A. I. (1992). Optimization of locomotion. In *Mechanics of Animal Locomotion* (ed. R. McN. Alexander). *Adv. Comp. Env. Physiol.* **11**, 277–300. Berlin: Springer Verlag.

Hoyt, D. F. and Taylor, C. R. (1981). Gait and the energetics of locomotion in horses. *Nature* **292**, 239–240.

Jenkins, F. A., Dial, K. P. and Goslow, G. E. (1988). A cineradiographic analysis of bird flight: the wishbone in starlings is a spring. *Science* **241**, 1495–1498.

Kvist, A., Klaasen, M. and Lindström, Å. (1998). Energy expenditure in relation to flight speed: what is the power of mass loss rate estimates? *J. Avian Biol.* **29**, 485–498.

Lilienthal, O. (1889). *Der Vogelflug als Grundlage der Fliegekunst*. Berlin: R. Gaertner; München: Oldenbourg. [Various editions. Annotated first edition reprinted Wiesbaden: Sändig, 1977; translated *Birdflight as the Basis of Aviation*. London: Longmans Green, 1911; St Petersburg, 1905, etc.].

Magnan, A., Perrilliat-Botonet, C. and Girerd, H. (1938). Essais d'enregistrements cinématographiques simultanées dans trois

directions perpendiculaires deux à deux à l'écoulement de l'air autour d'un oiseau en vol. *C. R. Hebd. Séanc. Acad. Sci., Paris* **206**, 462–464.

Marey, E. J. (1890). *Physiologie du Mouvement. Le Vol des Oiseaux.* Paris: G. Masson.

Masman, D. and Klaasen, M. (1987). Energy expenditure during free flight in trained and free-living Eurasian kestrels (*Falco tinnunculus*). *Auk* **104**, 603–616.

Norberg, U. M. (1985). Evolution of vertebrate flight: an aerodynamic model for the transition from gliding to active flight. *Am. Nat.* **126**, 303–327.

Osborne, M. F. M. (1951). Aerodynamics of flapping flight with application to insects. *J. Exp. Biol.* **28**, 221–245.

Pennycuick, C. J. (1968). Power requirements for horizontal flight in the pigeon *Columba livia. J. Exp. Biol.* **49**, 527–555.

Pennycuick, C. J. (1969). The mechanics of bird migration. *Ibis* **111**, 525–556.

Pennycuick, C. J. (1975). Mechanics of flight. In *Avian Biology*, vol. 5 (ed. D. S. Farner and J. R. King), pp. 1–75. London: Academic Press.

Pennycuick, C. J. (1989). *Bird Flight Performance: A Practical Calculation Manual.* Oxford: Oxford University Press.

Pennycuick, C. J. (1995). The use and misuse of mathematical flight models. *Isr. J. Zool.* **41**, 307–319.

Pennycuick, C. J., Klaasen, M., Kvist, A. and Lindström, Å. (1996). Wingbeat frequency and the body drag anomaly: wind-tunnel observations on a thrush nightingale (*Luscinia luscinia*) and a teal (*Anas crecca*). *J. Exp. Biol.* **199**, 2757–2765.

Phlips, P. J., East, R. A. and Pratt, N. H. (1981). An unsteady lifting line theory of flapping wings with application to the forward flight of birds. *J. Fluid Mech.* **112**, 97–125.

Poore, S. O., Sanchez-Haiman, A. and Goslow, G. E. (1997). Wing upstroke and the evolution of flapping flight. *Nature* **387**, 799–802.

Prandtl, L. and Tietjens, O. G. (1934). *Applied Hydro- and Aeromechanics.* London: Constable.

Rayner, J. M. V. (1979a). A vortex theory of animal flight. Part 2. The forward flight of birds. *J. Fluid Mech.* **91**, 731–763.

Rayner, J. M. V. (1979b). A new approach to animal flight mechanics. *J. Exp. Biol.* **80**, 17–54.

Rayner, J. M. V. (1985a). Flight, speeds of. In *A Dictionary of Birds* (ed. B. Campbell and E. Lack), pp. 224–226. Calton: T. & A. D. Poyser.

Rayner, J. M. V. (1985b). Bounding and undulating flight in birds. *J. Theor. Biol.* **117**, 47–77.

Rayner, J. M. V. (1986). Vertebrate flapping flight mechanics and aerodynamics and the evolution of flight in bats. In *Biona Report 5*, *Bat Flight – Fledermausflug* (ed. W. Nachtigall), pp. 27–74. Stuttgart: Gustav Fischer Verlag.

Rayner, J. M. V. (1988). Form and function in avian flight. *Curr. Orn.* **5**, 1–77.

Rayner, J. M. V. (1990). The mechanics of flight and bird migration performance. In *Bird Migration* (ed. E. Gwinner), pp. 283–299. Heidelberg: Springer Verlag.

Rayner, J. M. V. (1991). Wake structure and force generation in avian flapping flight. *Acta XX Cong. Int. Orn.* **II**, 702–715.

Rayner, J. M. V. (1993). On aerodynamics and the energetics of vertebrate flapping flight. In *Fluid Dynamics in Biology* (ed. A. Y. Cheer and C. P. van Dam). *Contemp. Maths* **141**, 351–400. Providence: American Mathematical Society.

Rayner, J. M. V. (1994a). Aerodynamic corrections for the flight of birds and bats in wind tunnels. *J. Zool., Lond.* **234**, 537–563.

Rayner, J. M. V. (1994b). Avian flight energetics in relation to flight speed and body size: discrepancies between theory and measurement. *J. Orn.* **135**, 302.

Rayner, J. M. V. (1995a). Dynamics of the vortex wakes of swimming and flying vertebrates. In *Biological Fluid Dynamics* (ed. C. P. Ellington and T. J. Pedley). *Symp. Soc. Exp. Biol.* **49**, 131–155.

Rayner, J. M. V. (1995b). Flight mechanics and constraints on flight performance. *Isr. J. Zool.* **41**, 321–342.

Rayner, J. M. V. (1996). Biomechanical constraints on size in flying vertebrates. In *Miniature Vertebrates* (ed. P. J. Miller). *Symp. Zool. Soc. Lond.* **69**, 83–109.

Rayner, J. M. V. (2000). On the origin and evolution of flapping flight aerodynamics in birds. In *New Perspectives on the Origin and Early Evolution of Birds* (ed. J. Gauthier). *Spec. Publs Yale Peabody Mus.* (in press).

Rayner, J. M. V., Jones, G. and Thomas, A. (1986). Vortex flow visualizations reveal change of upstroke function with flight speed in microchiropteran bats. *Nature* **321**, 162–164.

Rayner, J. M. V. and Swaddle, J. P. (1999). Aerodynamics and behaviour of moult and take-off in birds. In *Biomechanics and Behaviour* (ed. P. Domenici and R. W. Blake). London: Bios (in press).

Rayner, J. M. V. and Ward, S. (1999). On the power curves of flying birds. *Proc. 22nd Int. Ornl. Congr., Durban* (ed. N. J. Adams and R. H. Slotow), pp. 1786–1809. Johannesburg: BirdLife South Africa.

Smith, M. J. C., Wilkin, P. J. and Williams, M. H. (1996). The advantages of an unsteady panel method in modelling the aerodynamic forces on rigid flapping wings. *J. Exp. Biol.* **199**, 1073–1083.

Spedding, G. R. (1986). The wake of a jackdaw (*Corvus monedula*) in slow flight. *J. Exp. Biol.* **125**, 287–307.

Spedding, G. R. (1987a). The wake of a kestrel (*Falco tinnunculus*) in gliding flight. *J. Exp. Biol.* **127**, 45–57.

Spedding, G. R. (1987b). The wake of a kestrel (*Falco tinnunculus*) in flapping flight. *J. Exp. Biol.* **127**, 59–78.

Spedding, G. R. (1992). The aerodynamics of flight. In *Mechanics of Animal Locomotion* (ed. R. McN. Alexander). *Adv. Comp. Env. Physiol.* **11**, 52–111. Berlin: Springer Verlag.

Spedding, G. R., Rayner, J. M. V. and Pennycuick, C. J. (1984). Momentum and energy in the wake of a pigeon (*Columba livia*) in slow flight. *J. Exp. Biol.* **111**, 81–102.

Tobalske, B. W. and Dial, K. P. (1996). Flight kinematics of black-billed magpies and pigeons over a wide range of speeds. *J. Exp. Biol.* **199**, 263–280.

Torre-Bueno, J. R. and Larochelle, J. (1978). The metabolic cost of flight in unrestrained birds. *J. Exp. Biol.* **75**, 223–229.

Tucker, V. A. (1972). Metabolism during flight in the laughing gull, *Larus atricilla. Am. J. Physiol.* **222**, 237–245.

Tucker, V. A. (1973). Bird metabolism during flight: evaluation of a theory. *J. Exp. Biol.* **58**, 689–709.

Tucker, V. A. (1974). Energetics of natural avian flight. In *Avian Energetics* (ed. R. A. Paynter), pp. 298–334. Nuttall Ornithological Club.

Tucker, V. A. (1975). Flight energetics. *Symp. Zool. Soc. Lond.* **35**, 49–63.

Vest, M. S. and Katz, J. (1996). Unsteady aerodynamic model of flapping wings. *AIAA J.* **34**, 1435–1440.

Voigt, C. C. and Winter, Y. (1999). Energetic cost of hovering flight in nectar-feeding bats (Phyllostomidae: Glossophaginae)

and its scaling in moths, birds and bats. *J. Comp. Physiol.* B **169**, 38–48.

von Holst, E. and Küchemann, D. (1941). Biologische und aerodynamische Probleme des Tierfluges. *Naturwissenschaften* **29**, 348–362. [Translation: Biological and aerodynamical problems of animal flight. *J. R. Aero. Soc.* **46**, 39–56, 1942. (abridged) and *NASA Tech. Mem.* **75337**, 1980.]

von Mises, R. (1945). *Theory of Flight*. New York: McGraw-Hill [reprinted New York: Dover, 1959.].

Walker, G. T. (1925). The flapping flight of birds. I. *J. R. Aero. Soc.* **29**, 590–594.

Walker, G. T. (1927). The flapping flight of birds. II. *J. R. Aero. Soc.* **31**, 337–342.

Ward, S., Möller, U., Rayner, J. M. V., Jackson, D. M., Nachtigall, W. and Speakman. J. R. (1999a). Power requirement for starling flight in a wind tunnel. *Biol. Conserv. Fauna* (in press).

Ward, S., Rayner, J. M. V., Möller, U., Jackson, D. M., Nachtigall, W. and Speakman, J. R. (1999b). Heat transfer from starlings *Sturnus vulgaris* during flight. *J. Exp. Biol.* **202**, 1589–1602.

Weber, T. P. and Houston, A. I. (1997). Flight costs, flight range and the stopover ecology of migrating birds. *J. Anim. Ecol.* **66**, 297–306.

Welham, C. V. J. (1994). Flight speeds of migrating birds: a test of maximum range speed predictions from three aerodynamic equations. *Behav. Ecol.* **5**, 1–8.

Westerterp, K. R. and Drent, R. H. (1984). Flight energetics of the starling (*Sturnus vulgaris*) during the parental period. *Proc. 18th Int. Orn. Congr., Moscow*, pp. 395–398.

Wieselsberger, C. (1914). Beitrag zur Erklärung des Winkelfluges einiger Zugvögel. *Z. FlugTech. MotorLuft.* **5**, 225–229.

Winter, W. (1895). *Der Vogelflug: Erklärung der Wichtigsten Flugarten der Vögel mit Einschluss des Segelns und Kreisens*. München: Theodor Ackermann.

Withers, P. C. (1981). An aerodynamic analysis of bird wings as fixed aerofoils. *J. Exp. Biol.* **90**, 143–162.